

EXPEDITION REPORTS

Q115

G79

V. 3

Great Barrier Reef
Exped.

V. 3, 1569

LIBRARY
BUREAU OF COMMERCIAL FISHERIES
U. S. FISH AND WILDLIFE SERVICE
P. O. BOX 3830



Q115.G79
V.3

1569⁵⁹

GREAT BARRIER REEF EXPEDITION

1928-29

VOLUME III

BRITISH MUSEUM (NATURAL HISTORY)

GREAT BARRIER REEF EXPEDITION

1928-29

SCIENTIFIC REPORTS

VOLUME III



LONDON:

PRINTED BY ORDER OF THE TRUSTEES OF THE BRITISH MUSEUM

SOLD BY

B. QUARITCH, LTD., 11, GRAFTON STREET, NEW BOND STREET, LONDON, W.1; OXFORD UNIVERSITY PRESS,

WARWICK SQUARE, LONDON, E.C.4; H.M. STATIONERY OFFICE, LONDON, S.W.1

AND AT

THE BRITISH MUSEUM (NATURAL HISTORY), CROMWELL ROAD, LONDON, S.W.7

1930-1940

*Made and printed in Great Britain by
Adlard & Son, Ltd.
at their works, Bartholomew Press, Dorking*

CONTENTS

No.

1. A GEOGRAPHICAL INTRODUCTION TO THE BIOLOGICAL REPORTS. By J. A. STEERS. Pp. 1-15 ; 2 pls., 4 text-figs.
[Issued 22nd November, 1930.]
2. THE STRUCTURE AND ECOLOGY OF LOW ISLES AND OTHER REEFS. By T. A. STEPHENSON, ANNE STEPHENSON, GEOFFREY TANDY and MICHAEL SPENDER. Pp. 17-112 : 27 pls., 15 text-figs.
[Issued 25th July, 1931.]
- *3. DEVELOPMENT AND THE FORMATION OF COLONIES IN POCILLOPORA AND PORITES. PART I. By T. A. STEPHENSON. Pp. 113-134 ; 6 pls., 16 text-figs.
[Issued 15th August, 1931.]
4. OBSERVATIONS ON THE LIFE-HISTORY AND DEVELOPMENT OF THE HYDROID, *MYRIONEMA AMBOINENSE*. By ELIZABETH A. FRASER. Pp. 135-144 ; 3 pls., 6 text-figs.
[Issued 15th August, 1931.]
5. NOTES ON *TROCHUS NILOTICUS*. By F. W. MOORHOUSE. Pp. 145-155.
[Issued 23rd January, 1932.]
6. ON THE GROWTH OF THE ADULT COLONY OF *POCILLOPORA BULBOSA*. By S. M. MANTON. Pp. 157-166 ; 1 pl., 4 text-figs.
[Issued 25th June, 1932.]
7. GROWTH AND ASEXUAL REPRODUCTION IN CORALS. By T. A. STEPHENSON and ANNE STEPHENSON. Pp. 167-217 ; 10 pls., 14 text-figs., 9 tables.
[Issued 25th February, 1933.]
8. THE BREEDING OF REEF ANIMALS. PART I. THE CORALS. By SHEINA M. MARSHALL and T. A. STEPHENSON. Pp. 219-245 ; 1 pl., 6 text-figs., 3 tables.
[Issued 25th March, 1933.]
9. THE BREEDING OF REEF ANIMALS. PART II. INVERTEBRATES OTHER THAN CORALS. By ANNE STEPHENSON. Pp. 247-272 ; 14 text-figs., 4 tables.
[Issued 24th March, 1934.]
10. ECOLOGICAL SURVEYS OF CORAL REEFS. By S. M. MANTON, with Introduction by T. A. STEPHENSON. Pp. 273-312 ; 16 pls., 2 text-figs.
[Issued 27th July, 1935.]

* DEVELOPMENT AND THE FORMATION OF COLONIES IN POCILLOPORA AND PORITES, PART II.

When Part I of this report was written it was hoped that an anatomical study of the material preserved in Australia would reveal facts of importance connected with the development of the throat and mesenteric filaments in the Anthozoa, which have never been satisfactorily cleared up. In particular, it was hoped to test the conclusions arrived at by Krempf, which differ remarkably from those of other writers on Anthozoan development, and which were founded partly on *Pocillopora*. With this end in view a large series of whole mounts, sections and other preparations of the material was made, and considerable preliminary study undertaken. The result was to show that, so far as could be judged from the work completed, the stages needed for deciding the critical points are not present in the material. Two separate questions are involved : (a) the development of sexually produced planulae and (b) the development of asexually produced buds. The decisive stages for planulae are the very early ones, and it appears that all our planulae are much too old to give the information required. In the case of the buds, young stages are present, but are very difficult to interpret and throw no light on *sexual* development. It is clear that the mesenteries of both buds and planulae develop in couples bilaterally arranged about the directive axis, in the usual Anthozoan manner. Beyond this there is scope for the description of a certain amount of anatomical detail, but this would take an amount of time out of proportion to its value, and it was judged that the production of a further report would hardly be justified. The essentials of the story so far as this material will reveal it are contained in Part I.

A GEOGRAPHICAL INTRODUCTION TO THE BIOLOGICAL REPORTS.*

BY

J. A. STEERS,
St. Catharine's College, Cambridge.

WITH TWO PLATES AND FOUR TEXT-FIGURES.

(a) INTRODUCTORY: THE REEFS.

The "Great Barrier Reefs" extend in a nearly continuous series along the Queensland coast, from Torres Strait in the North to Swain Reefs in the South; approximately from 9° to 22° of south latitude. There is a further extension of the reefs to Lady Elliott Island in latitude 24° south, to the south-west of the Capricorn Channel. The "Barrier" is not an unbroken line of reef; only to the north of Cairns does it bear any very close resemblance to the Barrier Reefs of our text-books. In this part there is a chain of linear reefs facing the deep ocean, and intersected by narrow channels.

It is unfortunate that the system as a whole has been called the Great Barrier Reef, for south of Cairns, the so-called "Barrier" really consists of reefs spread over a wide platform, and showing no particular arrangement. The trends of the reef systems do not conform closely with those of the Queensland coast. In the extreme north the line of the outer barrier is some 80 miles from the coast; traced south to Cape Direction (13° S. Lat.), the outer reefs close with the coast, where their outer limit is only about 15 miles off shore. From here to the neighbourhood of Cairns ($16^{\circ} 55' S.$) the reef system is fairly regular, the outer edge varying between 20 and 30 miles from the coast, the inner edge approaching, at its nearest point, at Cape Melville within 7 miles. From Cairns southwards the "Barrier" progressively increases its distance from the coast, and the reefs composing it form an ever-broadening band. Near Townsville the reefs are about 50 miles away, and Swain Reefs are nearly 100 miles distant; the "Barrier" here being about 50 miles wide, and consisting of reefs, as yet largely uncharted.

The survey of the reefs is far from complete, but the existing Admiralty charts show their complexities extremely well. The characteristic outer reef zone in the southern part is several miles broad, and consists of an immense number of isolated patches of reef separated by channels, often too intricate and narrow for navigation. In the north

* Full accounts of the work of the Geographical Section of the Expedition will be found in the 'Geogr. Journ.,' lxxiv, 1929, pp. 232-257, 341-370; and vol. lxxvi, 1930, pp. 193-214, 273-297. By permission of the Royal Geographical Society, text-figs. 1, 2 and 3 are here reproduced from the former of these papers.

the outer line of the reef is clearly defined, and there is a steep slope to deep water, the 1000-fathom line being reached in a few miles. There are also wide passages through the "Barrier"; Trinity Opening off Cairns, is a good example. These wide openings, commoner in the southern parts of the reef area, have been associated by some writers with former river channels. There is very little *direct* evidence for this conclusion.

North of Trinity Opening some system may be traced in the reefs *between* the true outer barrier and the mainland. These reefs are isolated patches of varying magnitude, conforming in their general trends with the coast and the outer barrier. These "inner" reefs rise steeply from the floor of the protected sea, and many carry sand-cays on their surfaces. Between these inner reefs and the mainland there is a channel, for the most part free from obstructions, which forms the "Inner Route" for steamers visiting the Queensland ports. In this channel there are occasional "island reefs," which carry, in addition to a sand-cay, accumulations of shingle and a mangrove swamp. These are the Low Wooded Islands of the charts, and it was on one such, Low Isles, that the main expedition had its headquarters.

The individual reefs vary greatly in size and shape, but we may note here one or two *general* points. Nearly all reefs tend to develop a crescentic form, the convexity of the crescent facing the weather. In the case of an outer reef the convexity faces the Pacific; the inner reefs are convex to the south-east Trade. The reefs of the northern part of the outer barrier are long and narrow, their major axes running more or less north and south. Ribbon Reef is about 14 miles long. At their extremities they nearly always show landward-directed turns, thus conforming to the general crescentic form. Cairns and Arlington reefs are fine examples of reefs in which the convexity is directed south-east. Smaller reefs do not always show this appearance on the charts, but Low Isles, for example, shows an anchorage on the leeward side of the reef between the horns of the crescent. When the reef is exposed at a spring tide, this anchorage appears as a north-facing gulf or bay.

The protected sea which contains the detached reefs, is less than 200 ft. deep, except very occasionally in straits between high islands. Its floor is relatively very flat and covered with sediments derived from the mainland, islands and reefs and redistributed by marine agencies. As a rule, the increase in depth of this enclosed sea is gradual from the coast to the outer barrier, the average depth in the steamer channel being 15 to 20 fathoms.

The study of these numerous reefs is an enormous problem, mainly biological. The work of the Expedition, however, has amply demonstrated that much valuable work, in the way of careful surveys of the reefs and their debris accumulations, has yet to be done. Largely on account of physical difficulties this has not been attempted, but the time has come when a close and friendly alliance between workers in *all* sciences concerned with coral reefs is not only desirable, but necessary.

(b) THE PLATFORM ON WHICH THE REEFS REST.

It is one thing to describe and account for the biological phenomena associated with coral reefs; it is another to account for their origins. The Australian reefs are no exception. Of late years the tendency has been to go back to the Darwinian hypothesis of subsidence, largely through the work of W. M. Davis.* The importance of physiographical work is

* "The Coral Reef Problem," 'Amer. Geog. Soc.,' Special Publication, No. 9, 1928.

undoubted, and although analogies between different reefs and reef areas have much value, the present writer feels that each reef area needs careful individual study. This seems to apply particularly to the Australian reefs, which are developed on a much vaster scale than any others in the world.

In the scope of the present paper all that will be attempted is a short summary of some of the major problems relating to the origin of the reefs, or—what comes to the same thing—of the origin of the platform on which they are based. This will be followed by some generalized accounts of recent fluctuations of sea-level, and by a short summary of the main features of the high and low islands associated with the reef area, in so far as these problems affect the main point at issue.

A full discussion of the various hypotheses which have been put forward to explain the origin of the Australian reefs is out of place in these reports, and will be found in the reports of the Geographical Section of the Expedition published in the 'Geographical Journal' (see foot-note, p. 1).

The following account is designed to form a framework by which the biological work of the major part of the expedition may be related to the difficult problem of reef origins.

There have been many speculations as to the origin of the Queensland reefs, and, in brief, one may say that there are two schools of thought: the one regards the coralline mass as thick and as having grown up on a subsiding platform; the other thinks of the actual reefs as a comparatively thin veneer on a platform produced in some way quite independent of the reefs themselves. There are naturally variants of these hypotheses *e.g.* those who hold to a considerable thickness for the coral do not necessarily agree amongst themselves about the manner in which subsidence took place. Jukes and others think of a simple sinking of the Queensland littoral much in the manner Darwin postulated; others—and this is perhaps more typical of recent writers—think of warping, or foundering resulting from faulting of the eastern margin of the continent.

That submergence, to some extent, has taken place there is no doubt. The physiological evidence of the drowned valleys and certain borings on the mainland prove this. But a difficulty arises because submergence of a restricted amount can be explained without having recourse to the great downward movements such as are usually implied when thinking of the subsidence theory of coral reefs. It is probable that the relative level of land and sea oscillated through a range of some 200 ft. or more in the Quaternary Ice Age. Further, there is reason to believe that the Australian reefs are pre-Glacial in origin. If, then, we assume sea-level fluctuations of this sort in Quaternary times, and at the same time postulate (*cf.* Daly's Glacial Control Theory*) a lowering of ocean temperature, we may conceive of low level Pleistocene abrasion wholly or partially destroying any pre-Glacial reefs and cutting a platform not only around Queensland, but elsewhere. On this platform when both the temperature and level of the ocean rose once again, coral colonies grew and produced the reefs as we now know them.

But there are grave difficulties against accepting such a theory *in extenso*. Low-level abrasion of this sort clearly implies the production of cliffs. Cliffs are not entirely absent from the mainland coast and high islands within the barrier reefs. But what cliffs do exist are only of such magnitude as could be produced by the waves of the protected seas within the reefs. On the other hand, if there has been a post-Glacial rise of sea-level

* Daly, 'Proc. Amer. Acad. Arts Sci.', li, 1915, pp. 155–251, and 'Amer. Journ. Sci.', ser. 4, xli, 1916, pp. 153–186.

the cliffs which were produced at low levels are now drowned and probably buried by sediments, and it is highly doubtful if any evidence can be found for their existence.

However, apart from this difficulty, there are others of equal or greater magnitude. The great width of the platform on which the Australian reefs rest is, in itself, a strong argument against its complete production by low level Glacial abrasion. Also, it is not easy to see why there should be so many high or continental islands left standing as there now are if one assumes planation to this extent. Again, as Davis pointed out, any theory which regards the reefs as independent of, or subsequent to, the platform is faced with two difficulties—why should there be a long interval in time between the formation of the platform and the building of the reefs, and why should reefs only grow after the platform was formed?

But to argue against the probability of low-level abrasion in producing the platform is not to deny oscillations of sea-level. The evidence of the drowned valleys, etc., of the Queensland coast points to a relatively recent rise of sea-level of the order of 200 ft. We may take this as a post-Glacial rise. (It will be seen later that this is not the last movement of this type which has affected Queensland.)

A study of the geology and physiography of Queensland and the adjacent continental shelf south of the Cape York Peninsula shows clearly the importance of trend lines whose mean direction may be taken as north-north-west. Such trends are seen in many parts of the actual coast-line, in the various hill ranges, collectively grouped as the Coastal Ranges, in river courses, in lines of high islands and in certain parts of the reef area, *e.g.* the Capricorn Channel. Australian geologists have shown that such trends are approximately coincident with known anticlinal axes of Mesozoic Age and Tertiary fault lines. Sir T. W. E. David,* Prof. H. C. Richards and the late Charles Hedley,† W. H. Bryan,‡ D. R. Jardine§ and G. V. Stanley|| have called attention to the coincidence of fault lines with the present coast. Our own observations on the physiography of the coast, especially north of Cairns, bring us into line with this point of view.

In the Cape York Peninsula, Richards and Hedley claim that faulting has controlled the main outlines of the coast. But here the faulting has been rectangular, the main directions being east-west and north-south. A glance at the map (text-fig. 1) will make this point clear.

Other evidence for vertical movements is shown by the great gorges of the Barron and other rivers. These, in themselves, merely prove upward movement of the land, but it is highly probable that such movements, taken in consideration with the strongly faulted appearance of the mainland coast, especially north of Cairns, were accompanied by downward movements of that area which now lies beneath the protected seas.

The high or continental islands, which exist in large numbers between the reefs and the mainland, are frequently in lines, as already noted, approximating to the north-north-west trends, and show physiographical evidence of recent submergence. Such evidence of submergence as they show could possibly be explained by the recent sea-level rise of about 200 ft. But their physiographical evidence, and geological similarities to

* 'Journ. Roy. Soc. N.S.W.,' xlv, 1911, pp. 4-60.

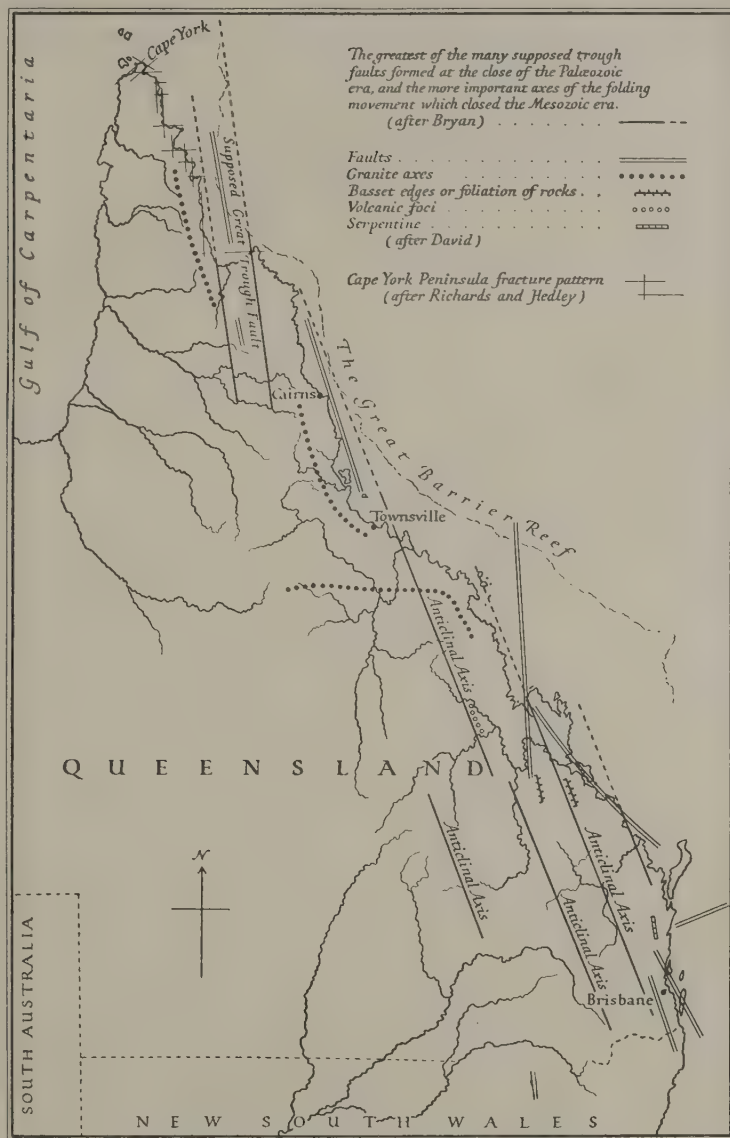
† 'Reps. Gt. Barrier Reef. Comm.,' i, 1925, pp. 1-28.

‡ 'Proc. Roy. Soc. Qd.,' xxxvii, 1925, pp. 1-82 (Pres. Address).

§ 'Reps. Gt. Barrier Reef Comm.,' i, 1925, pp. 1-51.

|| *Ibid.*, ii, 1928, pp. 73-110.

those parts of the mainland adjacent to them, suggest that they were separated from the mainland by a considerable submergence. Their actual appearance, as well as the strong suggestion obtained from a chart, leaves little doubt that they are partially drowned hill or mountain ranges.



TEXT-FIG. 1.—Tectonic lines in Queensland.

We thus arrive at the following position: Evidence seems to point to a recent submergence of the order of 200 ft., but, for the reasons given above, we can hardly think of the platform as having been cut entirely by low-level Pleistocene abrasion. If we consider the Tertiary tectonic movements which are known to have affected the eastern littoral of Australia, we have reasons for thinking that the downward movements which have affected the reef platforms have been considerable. At this point we come to a check.

In the present state of our knowledge we can only obtain direct evidence of subsidence by means of deep borings through coral reefs. Perhaps refined geo-physical methods of the future will allow us to obtain evidence of a reef's foundation more easily, but at present expensive borings alone are available. One of these bores was put down in 1926, on the larger cay on Michaelmas Reef. The result was rather disappointing. The cores have not yet been worked up. The bore reached a depth of 600 ft., and "The log shows that apart from a few feet of solid material, the coralline material was loosely coherent, that it extended to a depth of 427 ft., and that beneath this (apart from a little sand recorded from 477 ft.) down to a depth of 600 ft. there was nothing other than rounded quartz with abundant foraminifera, and shell fragments with much glauconitic material."

Hence we are left, unsatisfactorily, in the position of having to speculate upon the nature of the platform on which the reefs rest.

Andrews* is of the opinion that a peneplain was developed in Eastern Australia in the Eocene and Miocene periods. The present configuration of much of the Queensland coast bears out this point, and we may assume that this peneplain once existed over that part which is now covered by the reefs and protected sea.† It seems, then, that we must assume one of two things: either there has been a warping or flexing movement which has brought down this eastern part of the peneplain below sea-level, or that it has been faulted down. Which of these two views is more probable is largely a matter of opinion. The writer feels that the case for faulting, more or less parallel to the mainland shore, is stronger in view of the known evidence for Tertiary faulting in many parts, and also because the coast, especially to the north, has a faulted appearance. It would, however, be wrong to press this point too strongly.

But whichever view is taken, there is no need to assume that the downward movement has been equal in all parts of the Barrier area. There is also another difficulty: the shelf off New South Wales appears to be the unbroken continuation of that off Queensland, and presumably the two have much in common in their formation.

Another interesting point is that between Trinity Opening and the southern end of the Barrier Reefs, the 1000-fathom line, as far as can be seen from the general charts, runs far out to sea so as to include Osprey Reef, Diane Bank, Willis Islets, Lihou Reef and Cays, Marion Reef and Saumarez Reef. The 100-fathom contour includes Swain Reefs, and then conforms more or less with the general direction of the Queensland coast, and in the north follows closely the outer edge of the Barrier Reefs proper. From Osprey Reefs southwards to near Trinity Opening there is a deep water gulf of more than 1000 fathoms. Thus, the continental shelf of central Queensland, instead of falling steeply at the 100-fathom line to great depths, descends comparatively gently into a great protuberance enclosed within the 1000-fathom line, and for the most part covered by water less than 600 fathoms deep. The significance of this is not clear.

We must also notice another feature. If we do not assume a downward movement of the peneplain everywhere of the same amount, we must try to find an explanation of the more or less constant depth of the protected sea. It is probable that this may be associated with sedimentation. Dančs‡ and others have pointed out how much material

* 'Journ. Roy. Soc. N.S.W.,' xliv, 1910, pp. 420-480; and 'Proc. Linn. Soc. N.S.W.,' xxvii, 1902, pp. 146-185.

† For arguments on this point see 'Geogr. Journ.,' lxxiv, 1929, pp. 232-257, 341-370,

‡ Ann. Géogr., xxi, 1912, pp. 346-363.

has been deposited within the lagoon from rivers, currents and other sources. The redistribution of this material by marine agencies has almost certainly led to the equality of depths within the lagoon, and so in this way, even if the faulting or warping movements were unequal in their first effects, these inequalities are now no longer apparent, and we have the smooth-floored lagoon (apart from local exceptions near high islands), seen so well on the Admiralty charts.

It is regrettable that the basis on which a reef rests must largely be a matter of inference. It is, perhaps, the reason for the divergent points of view of biologists and geographers. The former are dealing with definite facts; the latter have too often to deal with theory. In so far, then, as the Australian reefs are concerned, we cannot go much further than saying that it is probable that they rest on a down-faulted or down-flexed peneplain of early Tertiary age, and composed of pre-Tertiary rocks, which once extended to the relatively steep declivity outside the outer Barrier Reefs. Later there were oscillations of sea-level associated with the Quaternary Glaciation, and apart from minor post-Glacial negative movements of sea-level, the last major phase was a positive movement amounting to about 200 ft., giving us the typical drowned valleys of New South Wales and Queensland.

No one is more aware than the writer that this leaves many points unexplained. The platform is of very variable width, especially in the south, where is the great indentation of the Capricorn Channel. Again, the evidence for faulting here is not so striking. In the north, the outer Barrier corresponds fairly well with the outer edge of the platform; in the south the reefs are more broken and scattered and no longer coincide with the margin of the platform nor can they, under any circumstances, be called "Barrier Reefs." In the present state of our knowledge it is not advisable to discuss the problem further in this place. The platform always has been, and for a long time will be, the centre of many theories, but, until we have much more detailed knowledge of the geology, in the broadest sense of the word, of Eastern Australia, and until we know much more about events in Quaternary times, and until Geophysics can tell us more about the probabilities of subsidence on a large scale, we must be content to leave the matter. Enough, however, has been said to make it clear that *no* simple explanation of the platform on which the corals, and so the biologists, have to work is forthcoming.

(c) RECENT RELATIVE MOVEMENTS OF SEA-LEVEL.

Mention has already been made of a relative movement of sea-level since the 200-ft. submergence. This last movement seems to have taken place in two stages of limited extent. Along the mainland coast of Queensland, and on some of the high islands, are traces of platforms of marine abrasion some eight feet above present mean sea-level. It is generally conceded that these fragmentary erosion surfaces point to a rise of the land, relative to sea-level, of some 18 to 23 ft. They have been noted by several writers, especially by Hedley. As these traces occur at much the same level, at widely separated places, we probably have to deal with a negative movement of sea-level, rather than with local land movements. This suggestion is strengthened when we note a lower platform more or less flush with the level of high-water neap tides. This lower platform is found all along the east Australian coast, within the Barrier area as well as far to the south in New South Wales. It is not the place here to enter into a discussion of the levels

at which such platforms are cut ; suffice it to say that writers differ a good deal in their views on this point. But there is a general consensus of opinion amongst those who know the occurrences of this platform in Queensland to ascribe it to a slight negative displacement of sea-level amounting to 12 + ft. or thereabouts. In other words, it appears that the total negative movement which has left these *two* platforms visible amounts to about 18 to 23 ft.

If such a conclusion be valid, it must have had interesting effects on the reefs themselves. How far this effect is demonstrable it is very difficult to say. But one or two points bearing indirectly on this problem must be noted. In the coral seas, beach sands and shingle are frequently cemented to form beach rock and coral-shingle conglomerates. Now on many islands, both high and low, such formations often occur at heights strongly suggestive of recent uplift, at least corresponding to the lower terrace of the mainland. Such occurrences are well seen on Houghton Island, Howick Island, Middle Island, Stone Island and many other places. These platforms are now being destroyed by marine erosion. If such uplifts have affected the low wooded islands of the protected sea, it is only reasonable to expect that the reefs themselves have been involved. It is, therefore, pertinent to draw attention to a point mentioned by M. A. Spender,* who gives reasons for believing that certain types of debris accumulations characteristic of the island reefs are possibly referable to this movement, which has elevated certain reefs so that shingle ridges (or ramparts) might be formed on them. Such a case is Low Isles. There remains, however, the difficulty of explaining why all inner reefs have not been equally affected. It is doubtful if this point can be answered, and the suggestion that such patches of reef, before the presumed fall in sea-level took place, had not all reached equal heights, clearly leaves us in as great a difficulty as before. The suggestion, however, stresses an important point. We need *precise* work on these reefs, work which will give us accurate maps of their surface structure (*cf.* the maps of Low Isles and Three Isles by Spender), and which will give us accurate measurements of mean sea-level. As experiments carried out during the Expedition amply showed, this is not an easy task, but it cannot be emphasized too strongly that such work is necessary. Whether or not this can ever be done on the outer Barrier remains to be seen, but until it is, it is extremely difficult to see how one can, if at all, say whether and how the outer Barrier has been affected by this negative movement. It is relevant at this point to note that certain reefs fringing the mainland, *e. g.* those near Port Douglas and Donovan Point, seem to have been exposed by this movement, and that their upper surfaces are now quite dead in so far as coral growth is concerned.

(d) THE HIGH OR CONTINENTAL ISLANDS.

Most of the islands within the Barrier belong to this category. A detailed account is out of the question, and only certain general matters need be mentioned.

They are formed of rocks in every way similar to those of the mainland, and are severed and partially drowned parts of the continent, pointing to a time when it extended to the east of its present limits. Some of these islands, or groups of islands, have been studied in detail by previous investigators, to whose accounts we must turn in order to see how the study of these islands bears on the general problem of the origin of the Reefs.

Most of these islands are covered with dense rain forest which may come down to

* 'Geogr. Journ.,' lxxvi, 1930, pp. 193-214, 273-297.

within a few feet of sea-level and continue to the summits, often more than 1000 ft. high. On the other hand, some islands have relatively few trees. Why this is so is not quite clear. Usually, between Townsville and Cairns, at any rate, islands of igneous rock seem to be rather more densely forested than others. The islands of metamorphic and sedimentary rocks farther north are often less densely forested, particularly in the Flinders group, which is formed of sandstone. In these northern parts the strong and persistent Trade must make it difficult for forest vegetation to thrive on the weather side of islands. In the south of the Barrier area the Whitsunday group is well forested, at any rate, on the slopes facing the mainland, but many other islands, *e. g.* the Beverley Islands, are grassy on their windward slopes.

"Many of the larger islands show evidences of dissection very clearly. They are cut up into deep valleys which radiate out from a single peak, or, if the island be elongate, the valleys furrow the longer sides."* These features have been well described by Stanley in the Whitsunday Islands. The most magnificent of the high islands is Hinchinbrook, about 70 miles north of Townsville, which has several peaks rising to more than 3000 ft. "There are deep gullies between these peaks. . . . It stands up as a great mountain mass, nearly equal in height to the mountains on the adjacent mainland. It is separated from the mainland by a narrow but deep and picturesque channel, now much contracted by mangroves fringing the mainland and the island shores of the channel. The island itself is divided by a low and broad valley into two parts, the southern, apparently largely of granite, being the higher and bigger. Here the peaks are truly mountainous and rugged, and afford the finest coastal scenery in the Barrier region. The northern part of the island contains Mount Pitt, a peak which reaches 2350 ft., but the outlines are less bold and rugged. This deep valley may be a structural feature, but not much is known of the geology of the island, and its densely forested nature makes it difficult to explore. However, the striking differences in profile between the northern and southern parts strongly suggest some differences in rock composition. . . ."

The seaward ends of the valleys and gullies of these high islands are nearly always filled with alluvium and silt, with forests, or mangrove swamps. In some cases (*cf.* Hinchinbrook) the mangroves form a nearly continuous border, and we may possibly have here another line of evidence pointing to the recent negative displacement of sea-level referred to above.

The slopes of many of these islands often continue unbroken to water-level, and when looking at a group of such islands, one cannot fail to be struck by their close similarity to drowned mountain ranges. The Palm and Whitsunday groups show this very clearly. Smaller islands stand up above the water as more or less rounded knobs, *e. g.* the Family Group. Some of these islands merely fringe the land, others, *e. g.* the Palm and Lizard groups, stand well away. North and South Direction Islands and the Lizard group are probably the most isolated, the nearest point on the mainland being some 16 miles distant.

The degree of cliffing to which these islands have been subjected is only moderate. Some of them are uncliffed; others possess minor bluffs, whilst a few are well cliffed. As noted above, the cliffing is only of such degree as could be caused by lagoon seas.

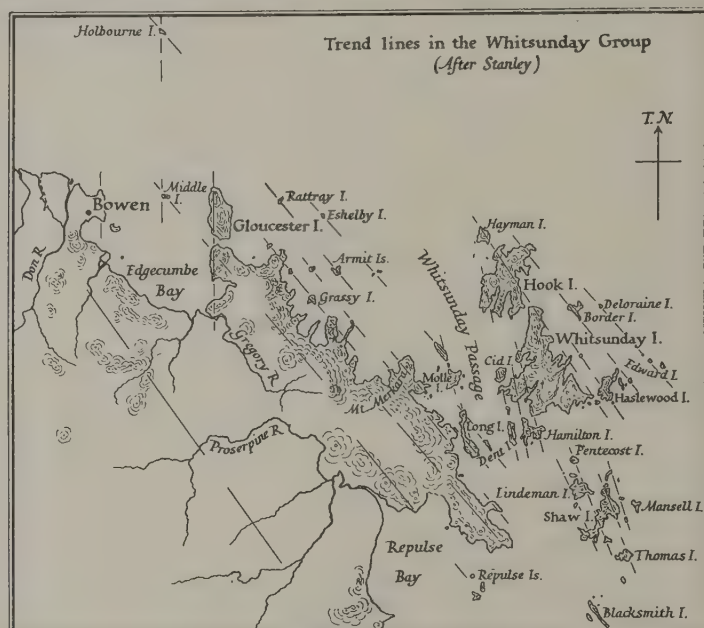
Flinders Islands, made of sandstone, show cliffing quite well. They are also rather

* Lines enclosed within inverted commas in this and the following sections are taken from the writer's account in the 'Geogr. Journ.,' lxxiv, 1929, pp. 232-257, 341-370.

barren and bleak. It has been shown* that they form part of an anticline which has been ruptured, the line of rupture being marked to-day by Owen's Channel.

Many islands possess fringing reefs: these, in their turn, have served to protect the islands from marine erosion.

It is obvious from a chart that many high islands are in lines, but such lines are not necessarily of structural significance. In some cases they are, as has been demonstrated by Stanley and Jardine in the Whitsunday and Keppel Bay islands respectively. Text-fig. 2 shows clearly the dissected nature of the Whitsunday group, and also the trend lines which Stanley has found in them. The detailed study of these islands is largely a matter of geology, but physiographically the degree of dissection they have attained, their "drowned"



TEXT-FIG. 2.

appearance, their trend lines, their benches, their cliffs, their mangrove flats and other features throw much light on their past history, and incidentally on that of the platform on which they stand.

(e) (1) SAND-CAYS AND (2) LOW WOODED ISLANDS.

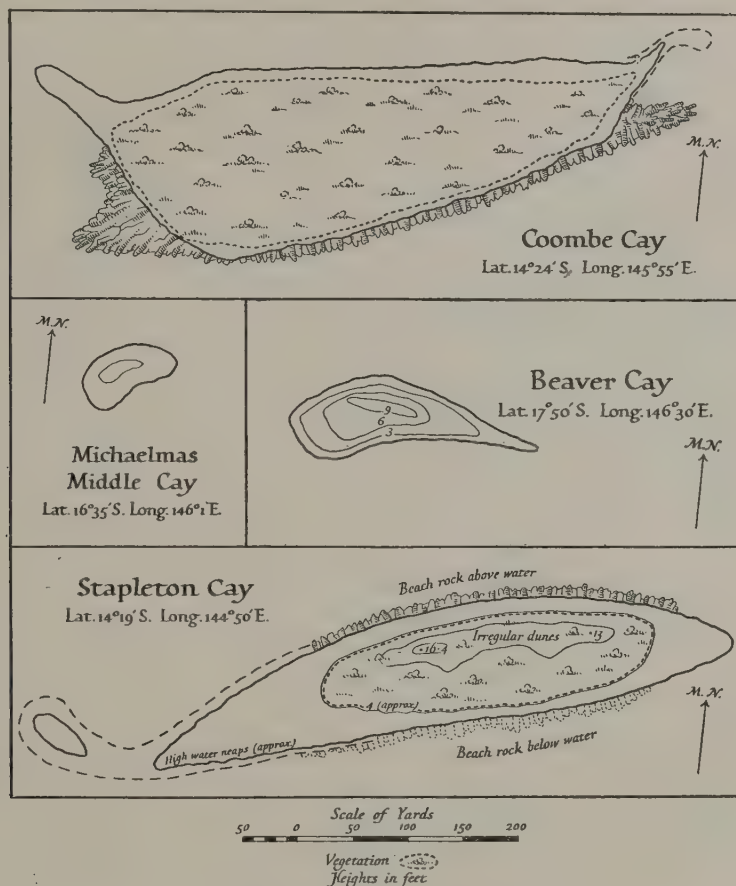
The "low islands" of the Reef area are of two types. The one consists of mounds of sand, known as cays, usually found on reefs situated near the outer barrier, the other we may call "Island reefs." These consist of a sand-cay on the leeward side of a reef, with an accumulation of shingle ridges, forming dry land and sheltering a mangrove swamp on the weather side of the reef.† These are the Low Wooded Islands of the Admiralty charts, and are found in, or near, the Steamer Channel (see p. 2). They do not appear to occur south of Trinity Opening, so that Low Isles is the southernmost of the series.

* Richards and Hedley, 'Reps. Gt. Barrier Reef Comm.', i, 1925.

† The shingle ridges (ramparts) are usually best developed on the windward side, but may extend so far to leeward as almost to meet the sand-cay.

(1) **SAND-CAYS.**—These simple cays are merely flat heaps of coral sand piled up on individual reefs. Their size and general appearance is shown in the accompanying figure of some typical examples. They do not usually exceed 4 or 5 ft. in height, above high water springs, and many are lower. In fact there is no real difference between a sand-bank awash at low water and a fully-developed cay.

Such structures are unstable, and vary a good deal in shape and size from time to time, with the varying incidence of wave-attack. Observations made on Beaver Cay* show how



TEXT-FIG. 3.—Typical Sand-cays.

easily and rapidly such changes take place. As a rule the cays are flat-topped, but in some cases vegetation has led to the growth of dunes and then the cays are higher and more irregular. The relations between vegetative and physical factors in the formation and growth of these cays is a matter which would repay full investigation. Some of the cays are entirely devoid of any plant life, others, *e. g.* Green Island, off Cairns, are large and well forested. There is every transition between these two extremes. However, the characteristic cay is usually covered by low shrubs, creeping plants or grasses, which have

* Beaver Cay, 'Qd. Geogr. Journ.,' xxxix (contribution No. 2, 'Reps. Gt. Barrier Reef Comm.'). Similar changes seem to have taken place on Pixie Reef,

led to the formation of dunes. Such cays, *e. g.* Michaelmas Cay, are usually the haunts of numerous birds. Once vegetation has obtained a hold the cays are rendered rather more stable. Another factor in their stability is the formation of beach rock around them. It is worth noting here that in all the cays we visited we did not find one in which there was beach rock* and no vegetation.

The position of the cays on the reefs on which they stand is important. Those which we visited were situated near the western or north-western end or leeward side of a reef. The longer axes of these cays were often oriented from a point rather to the north of east to one south of west, their longer axes being thus approximately at right angles to the prevalent south-east winds.

The coral sand which forms the cay is clearly the product of wave erosion of the reef on which the cay stands. This abraded material tends to be swept across the reef, mainly to the north-west. In many cases, doubtless, most of the material is swept completely over the surface of the reef, but in others another factor comes in. On the leeward side of some of the reefs the waves from the south-east often "wrap round" the reef, and the meeting of the two sets of waves is then instrumental in obstructing the travel of the material which is arrested and caused to accumulate on the reef. Later it is built up by waves into a cay. It is probable that the shape of the reef has very little to do with the resulting cay, which is quite independent of its foundation. The differences existing between the sand bank or immature cay and the relatively elaborate islands with forest trees, such as Green Island, seem to be accounted for mainly in two ways—age and exposure. "No direct evidence other than size and the stage to which vegetation and beach rock are developed suggests itself for determining the age of a cay, but it is a fact that the simplest cays are often in the more exposed places. This suggests that in many cases storms and other factors have prevented the cay from attaining any size, and, even more, have given such a cay a chequered career. It must be a matter of pure luck that a sand-bank evolves into a cay: the transition stages must often be long, and the embryo cay is doubtless often washed away, and growth has to begin all over again. Where, however, there is more shelter, growth may be more or less continuous and a fully-developed cay may result."

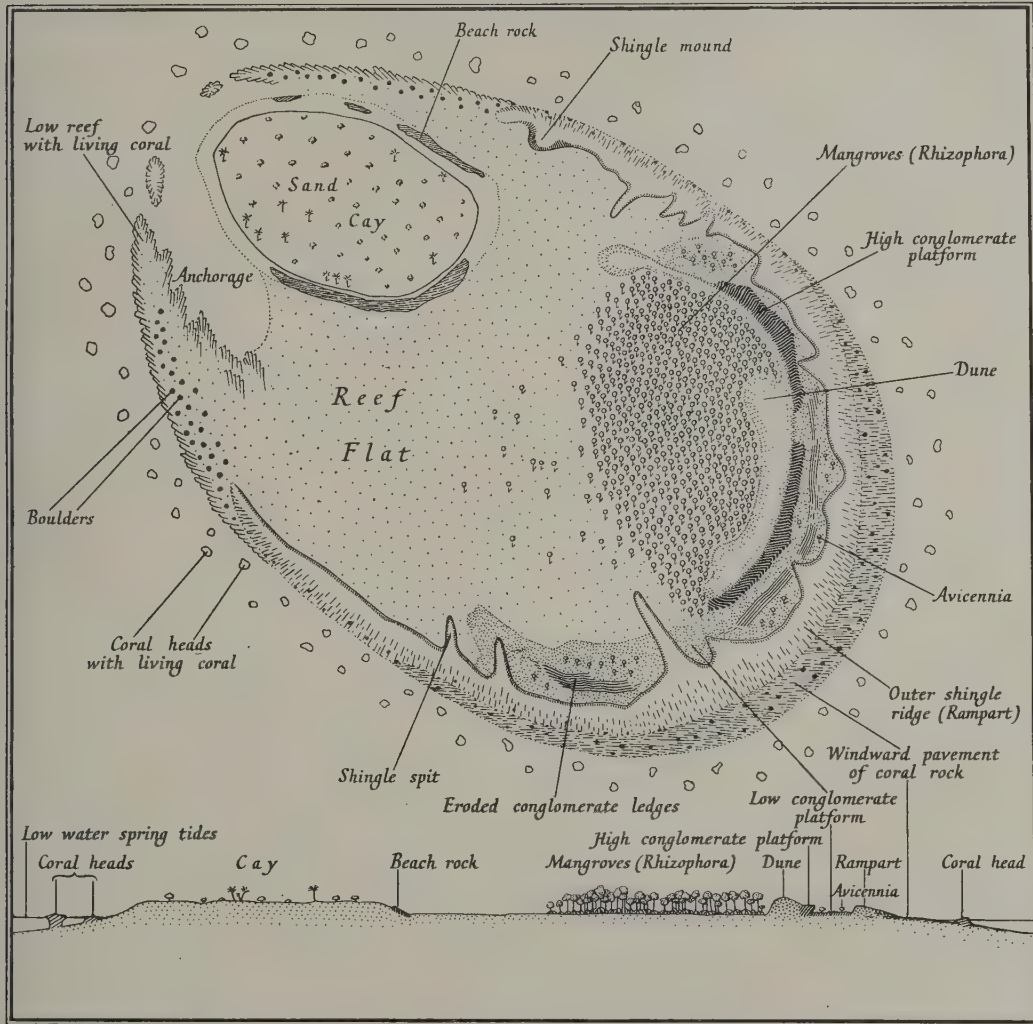
(2) LOW WOODED ISLANDS.—These are more complex, and offer some very interesting physiographical problems. In this paper general points only are considered, as the detailed maps and descriptions of Low Isles and Three Isles made by other members of the Expedition appear elsewhere.

The present account will be made clearer if reference is made to the accompanying figure. This figure, which bears a considerable resemblance to Three Isles, may be taken as a *generalized* representation of a Low Wooded Island, since it is based on a reconnaissance of several such islands. In the first place it will be noticed that the figure includes two distinct regions, one of which is a sand-cay, resembling in its essential features those just described; the other consists of a series of ridges or banks of shingle (referred to in these reports as *ramparts*), in the shelter of which lies a mangrove swamp. The two together make up the Low Wooded Island of the Admiralty charts. In the normal case both the sand-cay and the shingle and mangroves occur on the same reef, but at Hope Islands the sand-cay is on one reef, the shingle and mangroves on the other. Nevertheless we may consider the two as an entity.

* Michaelmas Cay carries vegetation, but no beach rock.

As the sand-cay so closely resembles the simple cays already described we need not give any further details here, beyond stating that it is normally more or less surrounded by beach rock, and that it usually possesses a covering of trees and plants.

The shingle "islets" are very different. There may be more than one of these, as at Three Isles, but in this case the two islets are really only discontinuous parts of a single



TEXT-FIG. 4.—Generalized sketch of a Low Wooded Island. (The vertical sides of the diagram may be taken as north-south lines.) Below is a section across the island.

series of structures. The same features, allowing for considerable individual variation, are found in all of them. On the windward side there is first the slope of the reef to deep water. Just within this we normally find ridges, or ramparts, of coral shingle. These ridges are not necessarily continuous; the outer are quite low, and slope gradually towards the sea, but steeply towards the mangroves. Inside the shingle ridges is a flat area, the *reef-flat*, which is covered at high water; and upon the surface of this flat, in the shelter of the inner ridges, lies the mangrove swamp. The shingle ridges often have narrow,

flat-topped tongues or spits running from their inner sides towards the mangroves. These, in some ways, resemble the shingle fans on the leeward sides of many shingle bars in this country, but the length, narrowness and flatness of many such on the low wooded islands renders them difficult of explanation.

The shingle ridges appear to rest upon a platform composed of coral rock, and part of this platform is visible as a rocky pavement, outside the ridges, at very low tides. This basal platform, which may be regarded as the essential "coral reef," upon which the other structures described are dependent, must not be confused with other rocky platforms at a higher level which may be found in connection with the shingle ridges. Two forms of this latter rock at least may be seen which it is reasonable to regard as stages in the development of former shingle ridges.* The first of these may be seen on the "Inner Rampart" at Low Isles, where the shingle has become compacted into a form of "shingle conglomerate"; the second at Three Isles, where there occur platforms of very hard rock which possibly represent part of a former shingle ridge or ridges which, after having become first shingle conglomerate and then a more compact form of rock, is now being eroded.

In a case like this, where uplift has occurred (see p. 8), these erosion features are intensified.

Frequently a conglomerate platform such as that of Low Isles shows a series of inclined layers, the dip of which is irregular, but often landwards. This must mean that considerable physiographical changes have taken place, *e.g.* the removal of protecting shingle ridges. If only a landward dip shows, one may, perhaps, conclude that the rest of a spit or ridge of shingle formerly existed to seaward.

On the inner edges of these conglomerate platforms, and presumably resting upon them, one normally finds a series, more or less continuous, of modern shingle ridges, which, in some cases, are covered with sand-dunes (as at King Island). Within this system of shingle ridges and shingle-conglomerate platforms lies the mangrove belt, which is being invaded by the shingle. Although certain mangroves are found outside the mangrove swamp proper, many of them belong to a species distinct from the one which constitutes the main population of the swamp (see the account by Stephenson and Tandy). "The mangrove belt proper is a gloomy region. It is intersected by channels and lagoons which sometimes dry out at low water, leaving an expanse of black mud. Here and there openings occur, and sometimes patches of dead mangrove, which give to the place a very sinister appearance. As elsewhere, the mangroves here are partly producing their own mud, and their ramifying roots are trapping the silt brought in by the tides. There is no hard and fast line of separation between the shingle ridges and the mangrove swamp." Some of the shingle tongues push right into the mangroves, either as narrow spits or as broad flat masses, which are really recurved termini. These are often colonized by true land plants, so that in the midst of a mangrove swamp it is no rare thing to meet a small patch of scrub vegetation.

As the shingle on the outer edges of the reef is subject to wave and tidal action, mainly from the quarter between south and east, it is often found that it is driven back to form two horn-like projections, so that the entire shape assumed by the complex of ridges is that of a crescent with its convexity towards the trade wind. This is well seen at Low Isles, where the small shingle mound to the east of the cay lies at the tip of one of the horns.

* For a fuller discussion on shingle ridges see M. A. Spender, 'Geogr. Journ.,' lxxvi, 1930, pp. 193-214, 273-297.

Between the sand-cay and the mangroves lies the reef-flat. This has been termed the "pseudo-lagoon" by some authors, but since it is in no sense a true lagoon, and simply the flat sandy top of a reef, the term "reef-flat" is adopted in these reports. At low tides this flat may dry out, only shallow pools being left upon its surface. Its surface is partly sand, partly rocky, and although the sand may extend right up to the edge of the mangrove swamp, it may be mixed with mud in this region, since the mangroves with their accompanying mud tend to spread out over the reef-flat towards the sand-cay. In many cases the reef-flat gives place on its leeward side to a deeper water zone, called the "Anchorage" (see Map of Low Isles).

In addition to the features already mentioned, large boulders, stranded by storms (Negro-Heads of some authors), are found on these reefs as well as on the outer barrier. They may occur on the windward side of inner reefs, but reach their maximum, in a case like that of Low Isles, on the leeward side of the reef, the side on which a sudden hurricane from the northward, coming in a direction opposite to that of the trade wind, does material damage to the unwieldy masses of coral accustomed to quiet water. As these islands and reefs are not exposed to the Pacific, the size of the boulders found upon them is fairly small.

If we take Low Isles as an example of the normal case of a low wooded island, we must put certain others in a separate category, *e. g.* some of the Turtle Group. The main point of difference between these and Low Isles is that the mangroves and accompanying shingle ridges are, as it were, closely wrapped round the sand-cay, the reef-flat thus being obscured. But, as in the normal case, there is a very distinct separation between the flora of the two "islets." Houghton Island, the second largest member of the Howick Group, shows similar features. Here, as in some other cases, a conglomerate platform is very well developed, and almost certainly has been upraised, *i. e.* it bears to this island, the same relationship which the low-level platforms already noted bear to the high islands and the mainland coast.

Why there should be no reef-flat between the two "islets" in these cases is not very clear. It may be that the reef on which the two are formed is too small to allow of the development of each separately, or perhaps it may mean that the mangroves have gradually spread over what was once a small reef-flat and so obliterated it. This movement has probably been accompanied by erosion on the windward side, which, in its turn, may have caused a pushing back of each successive zone.

It would seem, in either case, that the sand-cay precedes the shingle ridges and mangroves, because if we are right in assuming that the sand-cay is formed of detritus worn away from the reef, it is difficult to see how this process could go on effectively once the shingle and mangrove association has developed to windward. That the low wooded islands as a whole are characteristic of reefs some distance within the outer barrier is probably due to less wave action. The breakers of the Pacific on the outer reefs would probably be too powerful to allow of the development of shingle ridges piled above high water and, in turn, protecting a mangrove swamp.

DESCRIPTION OF PLATE I.

QUEENSLAND COAST AND THE GREAT BARRIER REEFS.

The following features referred to in the text are not shown in the map:

Diane Bank.

Between parallels $15^{\circ} 42'$ S. and $16^{\circ} 01'$ S., and longitudes $149^{\circ} 35'$ E. and $149^{\circ} 45'$ E.
(Approximately $15^{\circ} 50'$ S., $149^{\circ} 40'$ E.)

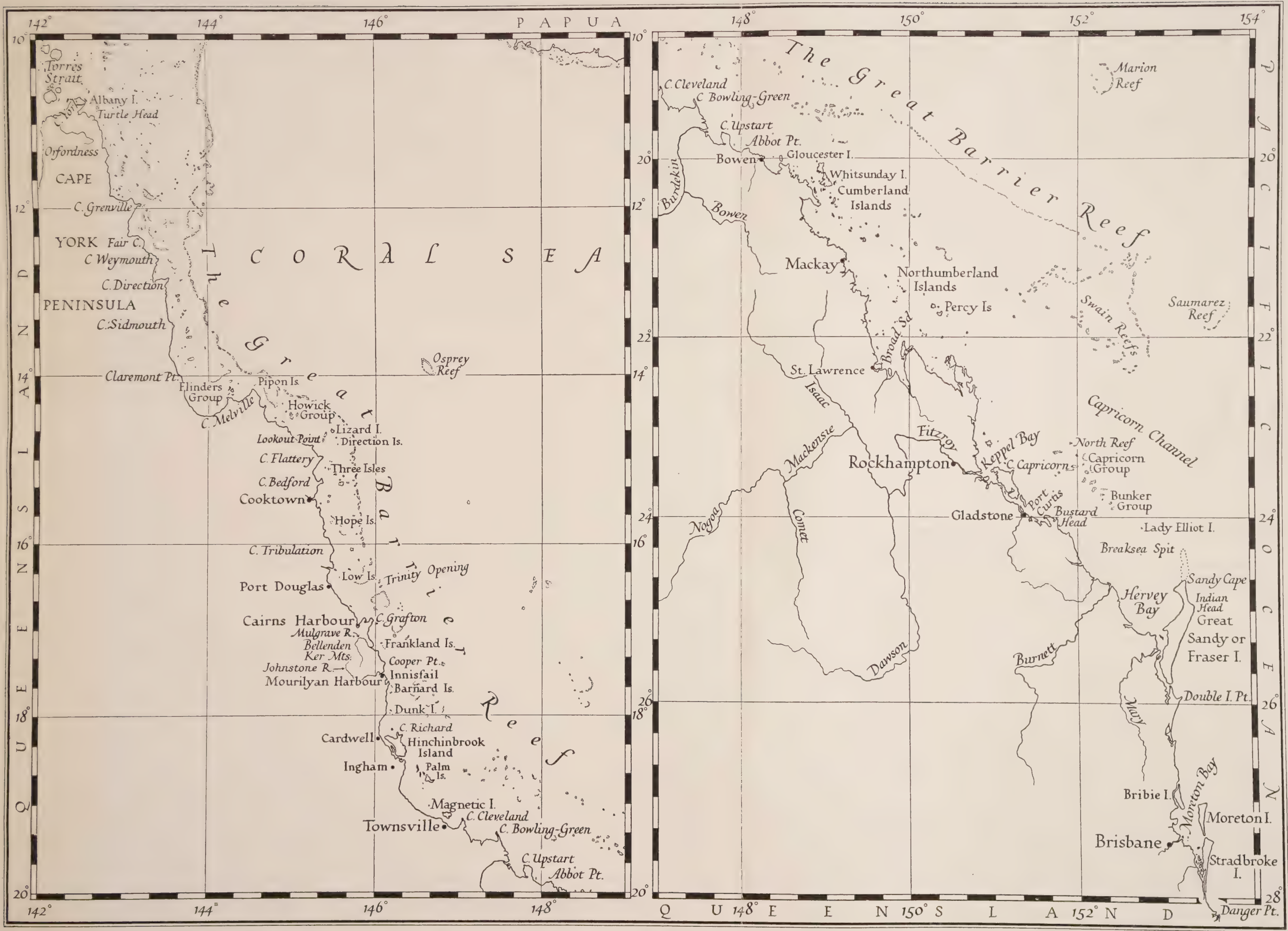
Willis Islets.

Between parallels $16^{\circ} 7'$ S. and $16^{\circ} 19'$ S., and longitudes $149^{\circ} 55'$ E. and $150^{\circ} 5'$ E.
(Approximately $16^{\circ} 10'$ S., 150° E.)

Lihou Reef.

Between parallels $17^{\circ} 7'$ S. and $17^{\circ} 39'$ S., and longitudes $151^{\circ} 17'$ E. and $152^{\circ} 13'$ E.
(Approximately $17^{\circ} 20'$ S., $151^{\circ} 45'$ E.)

(Approximate figures are the nearest round numbers to the middle of the bank.)





LIBRARY
FISH & WILDLIFE SERVICE
PACIFIC OCEANIC FISHERY
INVESTIGATIONS

THE STRUCTURE AND ECOLOGY OF LOW ISLES AND OTHER REEFS

BY

T. A. STEPHENSON, D.Sc., AND ANNE STEPHENSON

(*Department of Zoology, University of Cape Town*),

GEOFFREY TANDY, B.A.

(*British Museum, Natural History*),

AND

MICHAEL SPENDER.

WITH FIFTEEN TEXT-FIGURES AND TWENTY-SEVEN PLATES.

CONTENTS

	PAGE
PREFACE	17
PRELIMINARY DESCRIPTION OF THE REEFS	22
THE ECOLOGY OF LOW ISLES	35
REVIEW OF THE LOW ISLES FAUNA AND FLORA	69
COMPARISON OF THE ECOLOGY OF OTHER REEFS WITH THAT OF LOW ISLES	80
SUMMARY AND CONCLUSIONS	93
A COMMENT ON THE INSTRUMENTAL SURVEY	99
APPENDIX	101
REFERENCES	102
INDEX TO PLANTS AND ANIMALS	106

PREFACE.

(By T. A. STEPHENSON.)

THE ecological field-work upon which this paper is based was carried out under my direction by several members of the Expedition. The instrumental surveys of Low Isles and Three Isles to which we owe our knowledge of the physical features of these reefs were executed by M. A. Spender working for the Royal Geographical Society; he was assisted by Anne Stephenson and their results are embodied in Plates I and II.*

* For the presentation of data in the text-figures, however, and in those of the uncoloured plates, which are reproduced from drawings and not from photographs, I am responsible.



TEXT-FIG. 1 (for description, see p. 19).

The ecological work was carried out by the authors with the assistance of F. W. Moorhouse in the earlier stages and of E. A. Fraser, S. M. Manton and J. S. Colman later on. We are very much indebted to all these workers for their co-operation. We are also under a debt of gratitude to Mr. George Butler, of Townsville, owner of the motor-launch "Tivoli," to whose skill in navigation and other matters we owe the success of our visit to Lizard Island and the Outer Barrier; and to Mr. Wishart, of the yacht "Luana," who took us to Three Isles. Mr. T. C. Roughley has kindly allowed us to reproduce some of his photographs in our plates. Our work has also been greatly assisted by the very fine series of aerial photographs of Low Isles taken for us by the R.A.A.F. A mosaic from some of these is reproduced in Plate XXVII. To the Royal Geographical Society we are indebted for permission to reproduce Plates I and II, and Text-fig. 7, which (with the exception of the central section in Text-fig. 7) have appeared before in the Geographical Journal.

A short account of early references to Low Isles in the literature is given by Spender (1930, p. 212) elsewhere, and we need mention here only the facts that this island-reef was first mentioned by Cook in the journal of his historic voyage of 1770; and that the first investigators to visit it were J. Macgillivray and Thomas Henry Huxley, aboard H.M.S. "Rattlesnake" under Captain Owen Stanley, in 1848.

Since the whole work of the expedition was directed towards the elucidation of problems which have a direct bearing on ecology (*i. e.* towards a study of conditions and food-supply in the sea, of the feeding and metabolism of corals, of the growth and breeding of marine organisms, and so forth), it was clearly essential that the populations of the reefs themselves should be studied in such a way that, before correlating and applying the results of all the special lines of work, we should acquire a knowledge of what organisms form the bulk of these populations, and in what manner they arrange themselves with respect to one another and to their environment.

The descriptions of the distribution of organisms on the reefs are not the expression of individual opinions as to the nature of the populations, but are based upon a systematic survey carried out by several workers who wrote an agreed statement of their results at the end of each field excursion. Our examination of Low Isles was much more detailed than that of the other reefs; here the reef was divided up into small areas, and each of these was studied in turn by at least two workers, who made a description of each patch, and also lists and collections of the organisms found in it. The survey was therefore to some extent quantitative, and the personal element was eliminated as far as possible. The aims in collecting were (1) to secure a series of specimens of any common organism, the name of which was not certainly known, so that it might be identified later; (2) to obtain a representative collection of the common organisms, each labelled with some symbol indicating the exact area and habitat from which it came; this collection to be deposited in the British Museum for future reference, so that any statement of the

TEXT-FIG. 1.—Diagram of the Great Barrier Reef from Cook's Passage to Trinity Opening, showing the positions of the reefs described in this report, and suggesting the differentiation of the reefs into three series (Outer Barrier, Inner Reefs and Island Reefs), which is recognizable north of Trinity Opening (see p. 90). The High Islands are distinct from any of these series, being isolated mountains. Note the position of the 100-fathom line, which begins to diverge from the reefs just north of Trinity Opening. Modified from Admiralty Charts nos. 2923 and 2924.

occurrence of a given species on the reef should not depend on our word alone, but should be verifiable.

This method was designed for a general study of a wide area, and not for the precise estimation of the population of a small one. I therefore planned from the beginning to illustrate it by a series of accurate quantitative studies in chosen strips or patches of the main area. The result of such of these studies as we were able to make is recorded in a separate paper in this volume.

The general survey is subject to certain qualifications. The method outlined above could not be carried out as completely as we wished, because of the pressure of other work; but we believe it to have been sufficiently thorough to justify the account here given. Certain fields were perforce omitted from our scope. We could not give much attention to the concealed and commensal life of the interstices of coral platforms and of living corals; nor to the boring organisms; nor to the fishes; because any one of these would have occupied all the time at our disposal. But our omissions in these directions have been supplied to a considerable extent by G. W. Otter and G. P. Whitley. Some allowance must be made for the fact that the survey necessarily covered several months, and there would therefore be seasonal variations during its period. This is, however, probably of little importance from the point of view of this report, and mainly affects the size and number of some of the algae. Lastly, the omission of any extensive discussion of physical and chemical factors in the environment is intentional, since these will be treated fully in later papers dealing with the life and growth of corals.

There has been a tendency in recent years to regard the coral reef problem as one which is primarily of a geographical nature. The work of the Barrier Reef Expedition swings the centre of interest back towards the biological side, and our ecological study of Low Isles is a development of the methods by which the classical studies of coral reefs, such as those of Funafuti and the Maldives and Laccadives, were made; it is also in line with recent American work, and with that of Umbgrove and others. It is a method involving close collaboration between the surveyor of the physical features and the worker who is examining the plant and animal communities; and we feel that before it will be possible to review coral reefs in general with precision and security, this twofold point of view will need to be applied more widely.

There are several advantages to be derived from a careful study such as the one made at Low Isles. In the first place, only a detailed instrumental survey involving accurate measurements and determinations of levels can make it possible to form, after one's return from the field, a true conception of the inter-relation of the parts of a reef, both in the horizontal and vertical senses; and to describe accurately the distribution of organisms on it, especially as regards their zonation according to level and their relation to states of the tide. Secondly, such a study provides a real basis for the comparison of the reef with others; without exact data of distances, heights and populations, as well as details of the substratum, comparison must be a matter of uncertainty. Lastly, there is the advantage that anyone who has undergone the discipline of a detailed study of one reef, is thereby enabled to visit profitably other reefs which he cannot examine for more than a short time. His training has enabled him to appreciate rapidly the essential points involved, and to assess the relative importance of the surface-features accurately; whereas anyone without such experience is liable to be bewildered on a short visit to a reef, and to carry away no true impression of its formation. The incidence of the biological side of

the training lies in the fact that the differentiation of the zones and regions of a reef is often very subtle, and some pre-existing knowledge of the characteristic distribution and relations of common organisms may give a geologist or a geographer the key to some variation in the surface morphology of a reef which, though not easily appreciated at first sight, may be fundamental.

The lists of plants and animals presented in this paper, in connection with some of the regions described, make no pretence to be complete lists of the organisms found in the localities in question, nor even of the common ones. We could add to them extensively from our notes and collections; but have intentionally curtailed them because their object is purely illustrative. They are designed to convey in a summary form an idea of the series of organisms which characterize the various zones or areas, and this they effect as accurately in their present form as if they were extended.

Further information regarding the field-work upon which this paper is based may be obtained as follows by anyone desiring it: The data obtained by Spender during the instrumental surveys are deposited with the Royal Geographical Society, and include information not published either here or in the Geographical Journal. A set of prints of the aerial photographs of Low Isles is in the British Museum (Natural History), as also are the ecological collections. For further data referring to plants application should be made to G. Tandy, British Museum; for information referring to animals, to T. A. Stephenson, Zoology Department, The University, Cape Town.

For the identifications of the organisms mentioned in the report we are indebted to the specialists who have determined the collections for us, and who have been of great assistance to us in a variety of ways. The several groups have been determined by the following workers. I have worked carefully through all the collections of animals myself, after the identification of the species, in order to check and correlate the observations made in the field.

PLANTS.

FLOWERING PLANTS.—A. W. Exell, E. G. Baker, G. Taylor, J. E. Dandy and G. Tandy, British Museum.

ALGAE.—G. Tandy, British Museum.

ANIMALS.

PROTOZOA.—(Foraminifera). E. Heron-Allen, British Museum.

PORIFERA.—M. Burton, British Museum.

HYDROIDA.—E. A. Briggs, University of Sydney; and A. K. Totton, British Museum.

SCYPHOZOA AND ANTIPATHARIA.—A. K. Totton, British Museum.

ALCYONARIA.—S. J. Hickson, University of Cambridge.

ACTINIARIA and allied forms.—Oskar Carlgren, The University, Lund; and T. A. Stephenson, The University, Cape Town.

MADREPORARIA (and *Millepora*).—G. Matthai, Government College, Lahore; and T. A. Stephenson, The University, Cape Town.

NEMERTINEA.—H. A. Baylis, British Museum.

POLYCHAETA AND GEPHYREA.—C. C. A. Monro, British Museum.

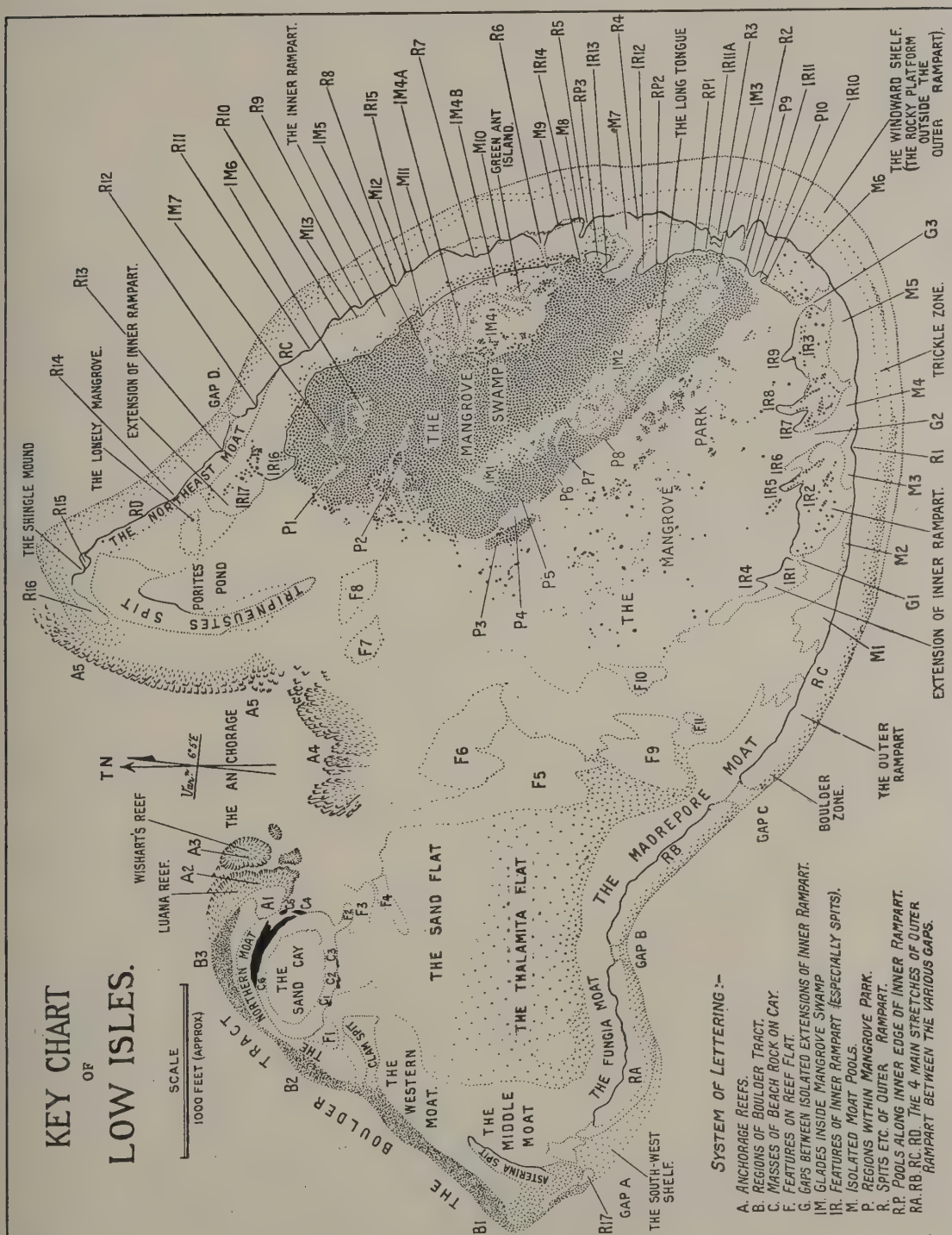
- OLIGOCHAETA.—J. Stephenson, British Museum.
 ASTEROIDEA.—A. Livingstone, Australian Museum.
 ECHINOIDEA, OPHIUROIDEA, HOLOTHUROIDEA AND CRINOIDEA.—H. Lyman Clark, Museum of Comparative Zoology, Harvard.
 CIRRIPIEDIA.—R. Bassindale, The University, Sheffield.
 ISOPODA.—M. H. Hale, The Museum, Adelaide, S. Australia.
 AMPHIPODA.—K. H. Barnard, S. African Museum, Cape Town.
 CRUSTACEA DECAPODA.—F. A. McNeill, Australian Museum; and Isabella Gordon, British Museum.
 HYMENOPTERA.—H. Donisthorpe, British Museum.
 LEPIDOPTERA.—N. D. Riley, British Museum.
 DIPTERA.—Daphne Aubertin, British Museum.
 ARACHNIDA.—Susan Finnegan, British Museum.
 GASTROPODA AND LAMELLIBRANCHIA.—T. Iredale, Australian Museum; and J. R. le B. Tomlin, British Museum.
 ASCIDIACEA.—Anna B. Hastings, British Museum.
 POLYZOA.—Anna B. Hastings, British Museum; and A. Livingstone, Australian Museum.
 ENTEROPNEUSTA.—Ethelwynn Trewavas, British Museum.
 PISCES.—G. P. Whitley, Australian Museum; and J. R. Norman, British Museum.
 AVES.—N. B. Kinnear, British Museum.

PRELIMINARY DESCRIPTION OF THE REEFS.

(By T. A. STEPHENSON, G. TANDY, and M. A. SPENDER.)

In order that the following description may be the better appreciated, two general influences should be kept in mind from the outset. The first is that of the tides. The tidal ranges may be accepted as the same for all the reefs to be considered. It is necessary when recording tidal variations to refer the level of the sea to the level of some fixed point. The fixed point (datum) which was used at Low Isles was that established during the survey by H.M. Surveying Ship "Penguin" in 1905. This was the level of the lowest available tide, and was measured as 17 ft. 2 in. below the level of the top of the step at the entrance to the Low Isles lighthouse. To this level all soundings and measurements of height recorded in this paper are referred. The highest tide measured on the continuously recording gauge employed by the expedition was 10 ft. above datum, and the lowest 0.4 ft. below it. The term "spring tide" will here be used to denote a tide which approaches the extreme range of 10 ft., and "neap tide" for one with a range of 2 ft. or less.

A second influence of prime importance is that of the prevailing wind (Text-fig. 3). For the period of twelve months during which our observations were made, the integrated mileage of wind recorded in the south-east quadrant is 85% of the total (a wind-rose is included on Plate I). During the summer months the south-east wind does not blow with any regularity, but there is no true reversal to a north-west monsoon. This is sufficient, for our purposes, to justify the use of the term "south-east trade wind."



The situations of the reefs to be described are indicated in Text-fig. 1. These were chosen for description because they illustrate the principal types of reef found within the area studied by the Expedition, and because, as will appear later, they seem to form an ecological series.

A. LOW ISLES. Lat. $16^{\circ} 23' S$. (Text-fig. 2 ; Plates I and III, etc.)

The name "Low Isles," in origin descriptive, was given to a small vegetated island together with a neighbouring mangrove-swamp, which are situated some seven miles from the mainland, and about 35 miles* north of Cape Grafton. The swamp and the island lie upon a single reef, and the name "Low Isles" will be used in this paper as referring to the whole system, including the reef itself and the structures upon its surface. The nearest of the large reefs of the Barrier series lies some seven miles to the eastward. Low Isles, therefore, is an isolated reef, situated in a shallow sea, and is not exposed to the surf of the Pacific. The sea in its immediate vicinity is from 8–14 fathoms in depth.

The reef has a major axis of about one mile, and the greater part of it is submerged at high water. It possesses a number of well-defined surface features, and these, both in form and orientation, express the dominating influence of the south-east trade wind. These regions, which are indicated in Text-fig. 2, will now be described.

1. THE SAND CAY.† (Plate IV, fig. 1.)

The islet on which the lighthouse stands. It lies at the leeward or north-western extremity of the reef, and is a flat-topped mound of sand, some $3\frac{1}{2}$ acres in extent, supporting a dry-land flora and fauna. Its greatest height is 16 ft. above datum.

2. THE MANGROVE SWAMP. (Plate V, fig. 1 ; Plate VI, figs. 1 and 2 ; Plate VII, figs. 3 and 4.)

An area covering about 50 acres, the greater part of which is thickly wooded with mangroves, of which *Rhizophora mucronata* is the dominant species. The woodland includes a number of glades or open spaces in which different conditions prevail.

3. THE SHINGLE RAMPARTS. (Text-fig. 7.)

A. *The Outer Rampart* (Plate XI ; Plate XII, figs. 1 and 2 ; Plate XIII, fig. 1).—A ridge of shingle consisting of dead coral fragments. This material is heaped up about the rim of the reef to form a band, shaped like a horse-shoe, with its convexity towards the south-east. The limbs sweep round to leeward, embracing the general reef flat upon which are situated the mangrove-swamp and sand cay. The inner edge of the rampart is sharply defined, forming a steep escarpment varying in height from about 2–4 ft. ; but towards the sea it slopes gradually downwards and merges into the seaward slope of the reef. It extends from the gap A of the key chart to the Shingle Mound, and in its south-eastern part it attains a height of $7\frac{1}{2}$ ft. above datum. Along the south-western margin of the reef it is lower, and is covered by tides rising 5 ft. above datum.

B. *The Inner Rampart* (Plate XII, figs. 1, 3, 4 ; Plate XIII, figs. 1–3).—In the space between the outer rampart and the mangrove swamp lies a second band of coral shingle

* Distances are given in sea miles.

† The word "cay" is derived from the Spanish "cajo," a shoal ; in the West Indies the derivative used is "key."

about 200 ft. wide, in form similar to that already described. It follows the trend of the outer rampart fairly closely, and is continued beyond the mangroves in either direction as patches or islands of shingle. It differs from the outer rampart in that the shingle is everywhere more or less compacted together by means of mud and silt which occupy its interstices. In the extreme case the shingle and mud is concreted to form a hard rock, which will be termed in this paper *shingle conglomerate*.

4. THE BOULDER TRACT. (Plate V, figs. 3 and 4.)

A band of boulders and large fragments of coral rock* extending from the western corner of the reef (B1 on the key chart) to the anchorage. It stands in the same relation to the reef-flat as does the rampart elsewhere. The boulders are frequently 3 or 4 ft. high.

5. THE REEF FLAT.

The whole area included by the outer rampart and the boulder tract. It is by no means uniform in structure and appearance. At the lowest ebb of a spring tide, the level of the flat is well above that of the sea outside the rampart; much of the eastern part is then 4 ft. above datum, or but little less (Text-fig. 7). Such parts of the flat as are not exposed at the ebb as wide sandy, rocky, or boulder-strewn expanses are covered by shallow water, which in places is as much as 2 ft. deep, but commonly much less. There are, therefore, discontinuous pools on the surface of the flat, but nothing exists which can be properly described as a lagoon. For convenience of reference, the flat may be subdivided as follows:

(a) *The Sand Flat* (Plate VIII, fig. 1).—An area of sand with shallow pools, continuous with the sand cay.

(b) *The Thalamita Flat*.—An area to the south of and not sharply delimited from the sand flat. Its characteristic feature is the presence of numerous slabs and boulders of coral rock with sand and small pools between them.

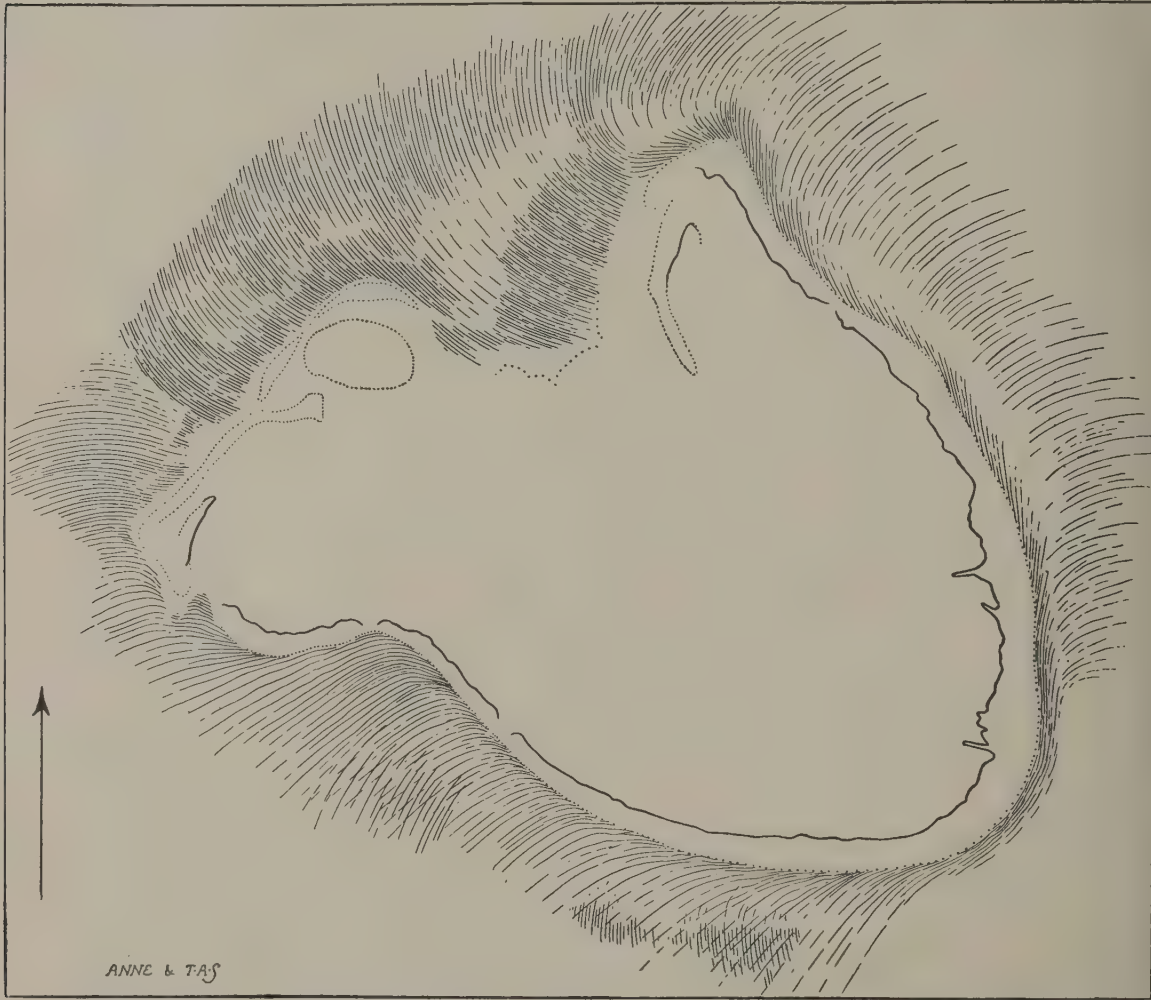
(c) *The Mangrove Park* (Plate XIII, fig. 4).—A large area to westward of the mangrove swamp, in which shallow pools predominate, and over which a considerable number of isolated trees of *Rhizophora mucronata* are distributed. Many of these are young, and there are also clumps of fairly large trees; but they nowhere attain the dense formation characteristic of the mangrove-swamp proper. The ground is partly sandy, partly overlaid by flattened and much honeycombed coral rock; and is for the most part more or less thickly colonized by a flowering plant with grass-like leaves (*Thalassia Hemprichii*), with which other plants mingle to form a turf.

(d) *The Moats* (Plate VIII, fig. 3).—A linear series of pools lying immediately within the outer rampart or the boulder tract. They are nowhere more than about 18 in. deep at low water. Inside the boulder tract and the western part of the outer rampart, these pools form a single continuous moat or band of water; but from the southern extremity of this band onwards (following round the rampart in an anti-clockwise direction) the moat becomes much interrupted, and is represented only by a chain of discontinuous pools until it re-emerges, near the northern extremity of the mangrove swamp, as a second band-like sheet of water (the north-west moat). The several regions of the western and principal stretch of the moat have been given individual names (Northern Moat, Western Moat, Middle Moat, etc.) for convenience of reference.

* A list of the types of rock mentioned in this report will be found in the appendix, p. 101.

6. THE ANCHORAGE (Plate XIV, fig. 1).

A bay or indentation in the northern side of the reef. It has depths of 10 to 20 ft. below datum, a sandy bottom, and is fringed by reefs supporting a rich growth of living coral.



TEXT-FIG. 3.—A diagrammatic representation of the effect produced by the Low Isles Reef upon the waves driven against its windward arc by the south-east trade wind. This figure throws light upon (a) the general shape of the reef, and (b) the formation of the cay, which appear to be due to the united effects of the system of waves here shown, and of the eddy set up in the lee of the reef by the general drift of water before the south-east trade, especially on the flood tide. The data are obtained from a series of aerial photographs taken by flight 101 of the R.A.A.F. in September, 1928.

It will be appreciated that at high water of springs the entire reef flat is covered by about 6 ft. of water. Only the upper part of the sand cay and the main foliage of the

mangroves then appear above the sea, the two being separated by a broad sheet of water. The general aspect of the system at low water of springs is very different; the sand cay is then a hummock from which one can descend on to the reef flat and walk across to the mangroves, or to the south-eastern corner of the reef. The rampart has emerged from the sea and can be seen encircling the reef as a low wall, rising to 10 ft. above datum at its north-eastern extremity in the Shingle Mound (Plate XII, fig. 2).

All tides do not ebb to the same level, and this fact conditions the amount of the anchorage and seaward slope accessible at low water. The zones of rich coral growth are exposed at extreme low tides only. During the winter months (May to October) the lowest tides occur during the daytime, for several days in each month, towards the time of new moon. In the summer the opposite is the case, the lowest tides occurring at the time of full moon, and at night. Extreme exposure, therefore, never occurs in daylight during the hottest weather.

B. THREE ISLES. Lat. $15^{\circ} 07' S.$ (Plate II.)

Three Isles is a group of three low islets lying some 8 miles NE. by N. of Cape Bedford. These islets are part of a single reef-system directly comparable with that of Low Isles. The system lies about 80 miles north of Low Isles, and is similarly situated with respect to the mainland and to the Barrier Reefs, the mainland lying about 10 miles to the westward and the inner reefs of the barrier some 4–6 miles to eastward. The protected sea surrounding the reef is of the same depth as at Low Isles, the tidal range and establishment are similar, and the south-east trade wind is equally dominant, though fresher and more persistent.

In essential form Three Isles and Low Isles are so much alike that the resemblance can be traced in some detail. The plan of Three Isles is ovate, the broad end to windward. In this it is probably a more usual and regular example of the class of reef to which it belongs than Low Isles, which possesses, in its western salient, a feature peculiar to itself. The apparent difference between individual features on Three Isles and Low Isles is in some cases considerable, but a close analysis reveals their essential similarity; the regions will be considered under the same headings as for Low Isles.

1. THE SAND CAY.

The sand cay is about 36 acres in extent and about 3 or 4 ft. higher than that of Low Isles.

2. THE MANGROVE SWAMP.

At its northern end this lies close to the sand cay. It covers some 41 acres, and its limits are very clearly defined. The whole inner structure of the area is not known, but it contains glades similar to those at Low Isles. As will be obvious from the figures given, the mangrove swamp is smaller than that of Low Isles, whilst the cay is considerably larger.

3. THE RAMPART.

This is less well developed than that of Low Isles; it is nowhere very high—probably rarely more than 5 ft. above datum. It is somewhat broken in the south-eastern part of its circuit, where the counterpart on Low Isles is particularly free from interruption.

Since the shape of a rampart and the form of its terminations are conditioned by the plan of the reef upon which it lies, the rampart at Three Isles follows a smooth curve without such abrupt changes of direction as are associated with the embayment opposite the gap B, and with Asterina Spit and the Shingle Mound on Low Isles.

4. THE BOULDER TRACT.

The difference in the form of the leeward margin of the reef is responsible for a boulder tract of somewhat different character from that of Low Isles. A region containing boulders and fragments occurs, however, where the reef-margin faces a direction between north and west, as at Low Isles.

5. THE REEF FLAT.

This is of the same essential nature as the Low Isles reef flat, but differs from it in some details. It is more extensively covered with water when the tide has ebbed than the flat of Low Isles, but shows a subdivision into regions comparable with the Sand flat and the Thalamita flat. There is no region at Three Isles comparable to the mangrove park at Low Isles, since the mangrove swamp ends on its western side in an almost unbroken wall of trees with no outliers. The moat at Three Isles differs from that at Low Isles in the facts that it is more broken up into sections and has a less flourishing coral fauna.

6. THE ANCHORAGE.

A small inlet with a sandy floor, fringed by reefs supporting a rich growth of coral, and situated to the north-west of the cay, undoubtedly corresponds to the anchorage of Low Isles, although it exists in a reduced form and is differently related to the cay.

Apart from the regions already described, Three Isles possesses the following features which are without exact correspondence at Low Isles.

1. THE DUNE. (Plate XXII, fig. 3.)

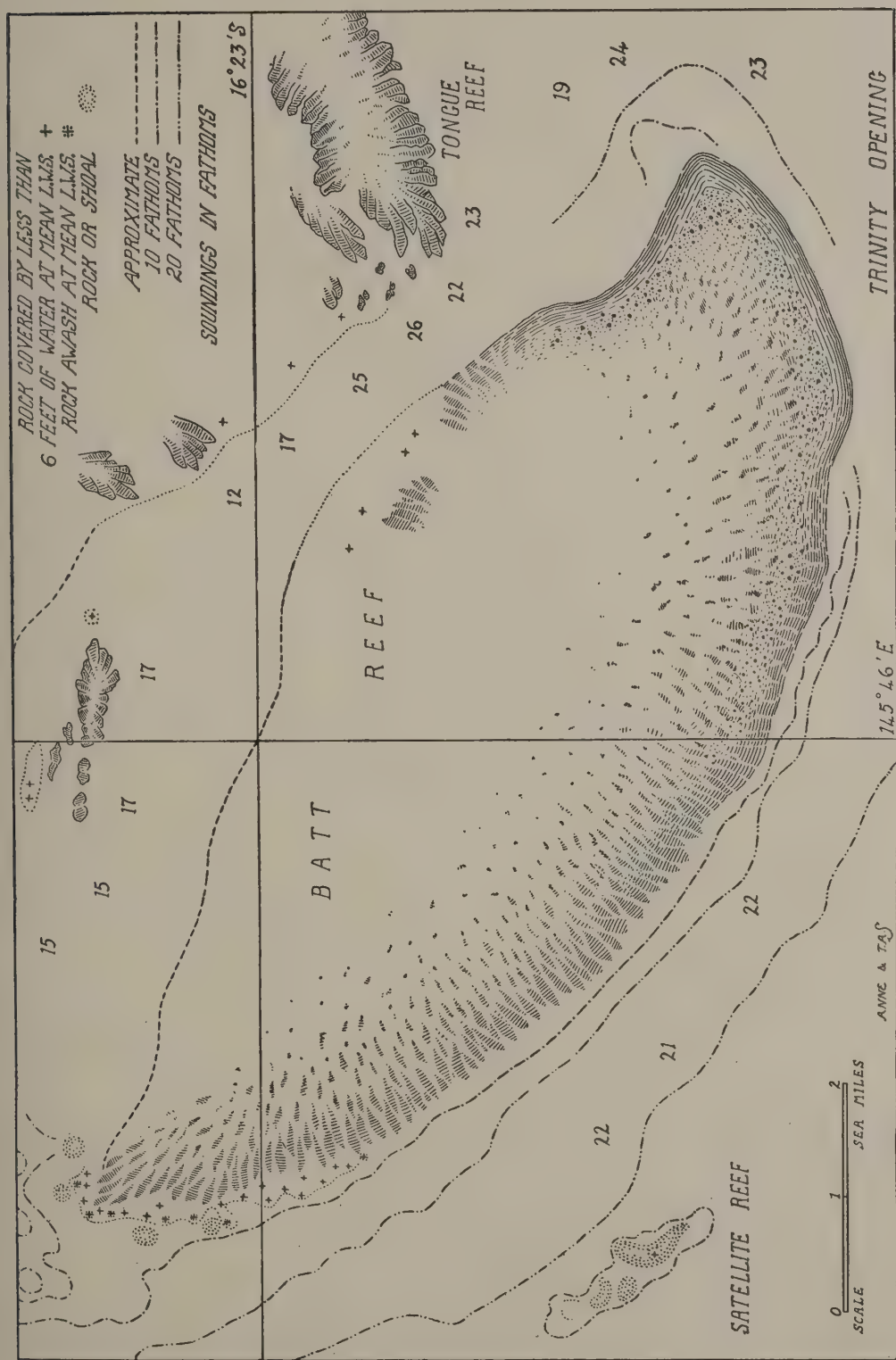
In the south-eastern part of the reef, along the greater part of the seaward edge of the mangrove swamp, there is an accumulation of shingle, sand and pumice forming a dune-like bank about 50 yds. wide and probably as much as 20 ft. above datum at the summit. The inner edge descends steeply into the mangrove swamp, and the district supports a dry-land fauna including characteristic dune plants. At Low Isles nothing of this sort exists, but there is a narrow shingle-ridge in a corresponding position.

2. CASUARINA SPIT.

A spit of clean coral shingle situated at the northern end of the mangrove swamp, and supporting a dry-land flora in which the dominant tree is *Casuarina equisetifolia*.

3. THE THIRD ISLAND. (Text-fig. 14; Plate XXII, fig. 2; Plate XXVI, fig. 1.)

An area about 900 ft. long and 180 ft. wide, of complex structure. Along its western side runs a platform of hard coral rock. This is much eroded and pot-holed, its seaward edge is cliff-like, and the general level of the surface is such that it is covered at spring tides. East of the rocky platform there is a band of compacted shingle and debris, supporting a flora of grass and bushes, and followed by a ridge of clean shingle. Between this and the flat is a line of *Rhizophora*.



TEXT-FIG. 4.—Batt Reef. This figure is modified from Admiralty Chart no. 2924, and summarizes the knowledge of the reef gained by the Expedition. The representation is purely conventional, since the extent of the pavement indicated by parallel shading round the windward angle of the reef is not known. The unshaded part of the reef represents sand.

4. THE PROMENADES.

The seaward margin of the dune leads down to the surface of a platform, in places about 60 ft. wide, of a hard coral rock similar to that of the Third Island. The surface is pitted and pot-holed, and the often precipitous or overhanging outer edge is undercut in places. The platform is subdivided into two somewhat different regions, as follows :

(a) *The High Promenade* (Plate XXII, fig. 1).—In the south-eastern part of its extent, the top of the platform is as much as $5\frac{1}{2}$ ft. above the level of the low pavement which lies between it and the rampart. There are two interruptions in its course, but its essential continuity for about 1300 ft. justifies its consideration as a separate morphological unit.

(b) *The Low Promenade*.—The northern part of the platform is also more or less interrupted in its course ; it is similar in structure to the high promenade, but considerably lower in level.

Where the margin of the dune overlies the promenades, there is a narrow beach of sand and coral shingle which is continuous, at its northern extremity, with Casuarina Spit.

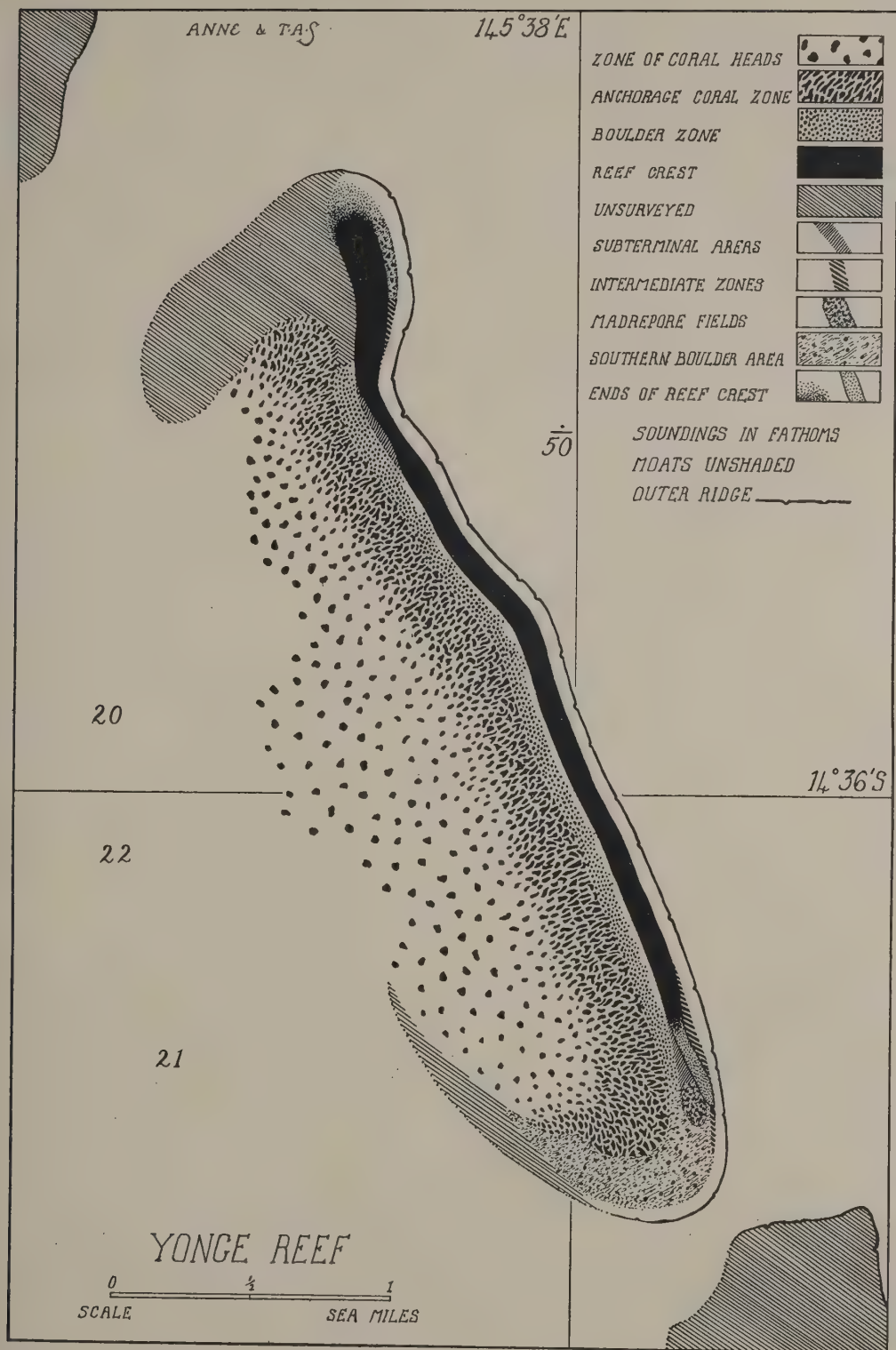
C. BATT REEF. Lat. $16^{\circ} 23' S$. (Text-fig. 4 ; Plate XXVI, fig. 2.)

We are unable to give a detailed account of Batt Reef, since it covers an enormous area and is incompletely surveyed, nor were we able to work there sufficiently often. It is about 10 miles long and 4 miles wide, its major axis running about ESE. to WNW. Its north-western corner lies some 7 miles east of Low Isles. The western side of the reef faces the protected sea between Barrier and mainland, and its southern shore flanks Trinity Opening. There is a sharp angle at the south-eastern extremity, and from here northwards until it becomes protected by Tongue Reef the edge is open to the Pacific. Batt Reef has the form of a distorted crescent with its convexity directed south-eastward.

The surface appearance of the central part of Batt Reef is that of a vast sand-flat. At a point visited close to the acute south-eastern extremity the seaward slope consists of a rocky marginal pavement, which passes, without any intervening rampart, into a region closely resembling the Thalamita Flat at Low Isles. There is no deep water inside the arms of the reef, which therefore contains no lagoon but only a central sand-flat. The north-western part of the reef-margin has no rocky boundary, but is much broken up into reef patches. Batt Reef uncovers only at spring tides.

D. YONGE REEF. Lat. $14^{\circ} 36' S$. (Text-fig. 5 ; Plate XVII, fig. 2 ;
Plates XXIII and XXIV ; Plate XXVI, fig. 4.)

Yonge Reef was chosen for careful examination because it appeared from the chart to be a characteristic reef of the Outer Barrier series, and was accessible from a temporary base which we established on Lizard Island. Brief examinations of other reefs (Ribbon Reef, Ruby Reef, Escape Reef), which seemed to be of the same class, confirmed the supposition that although there is considerable variation within the class, Yonge Reef might be regarded as typical. It is a reef quite unlike either of the types which we have hitherto described. It is about 4 miles long, a mile wide, has its major axis directed nearly NNW. to SSE., and is separated from similar reefs in the same series by narrow channels at its northern and southern ends. The reef therefore is of elongate form, and its most



TEXT-FIG. 5.—Diagrammatic representation of Yonge Reef. The size, outline and orientation are taken from Admiralty Chart no. 2923. The relative widths of the zones along the oceanic side were obtained from pacings along a transverse section. The remaining details are sketched in, and the sizes and relations of the small areas near the ends of the reef are very approximate.

solid surface feature, a band-like pavement of rock along its Pacific border, forms a low barrier upon which the energy of the breakers expends itself, their attack being moderated, but rarely ceasing even in calm weather. At the extremities of the reef the margin turns inward towards the mainland, forming two recurving horns, whose course becomes parallel to that of the main body of the reef before they terminate. The area contained within this crescentic margin includes innumerable coral heads and reef-patches, but it is possible to work a boat among them. The reef has no continuous western boundary apart from the recurving horns already described. Its Pacific slope descends rapidly to deep water.

The greater part of the length of the reef (leaving out of account, for the moment, its modified terminal regions) is differentiated into a series of band-like zones, running parallel to one another in the direction of its long axis. The zones have been designated as follows :

1. THE REEF CREST. (Plate XXIII, figs. 1, 3 and 4.)

A pavement of solid coral rock, swept clear of debris, over 3 miles in length and some 160 yds. in breadth. Its general level is slightly higher than that of the surrounding regions, and it constitutes, as it were, the backbone of the reef.

2. THE OUTER MOAT. (Plate XXIII, fig. 1.)

Proceeding from the reef-crest towards the Pacific, one traverses first a moat. The floor of this moat slopes gently downward from the reef-crest to the deepest part, which lies immediately to landward of a second and lower ridge (THE OUTER RIDGE) not far from the breakers. The moat is in many places partly filled up by irregular masses and platforms of coral rock, some of which are continuous with the outer ridge ; but in the main it is well marked, attaining a depth of some 5 ft. in places, close to the outer ridge. Its width is about 100 yds.

3. THE OUTER RIDGE. (Plate XXIII, fig. 2.)

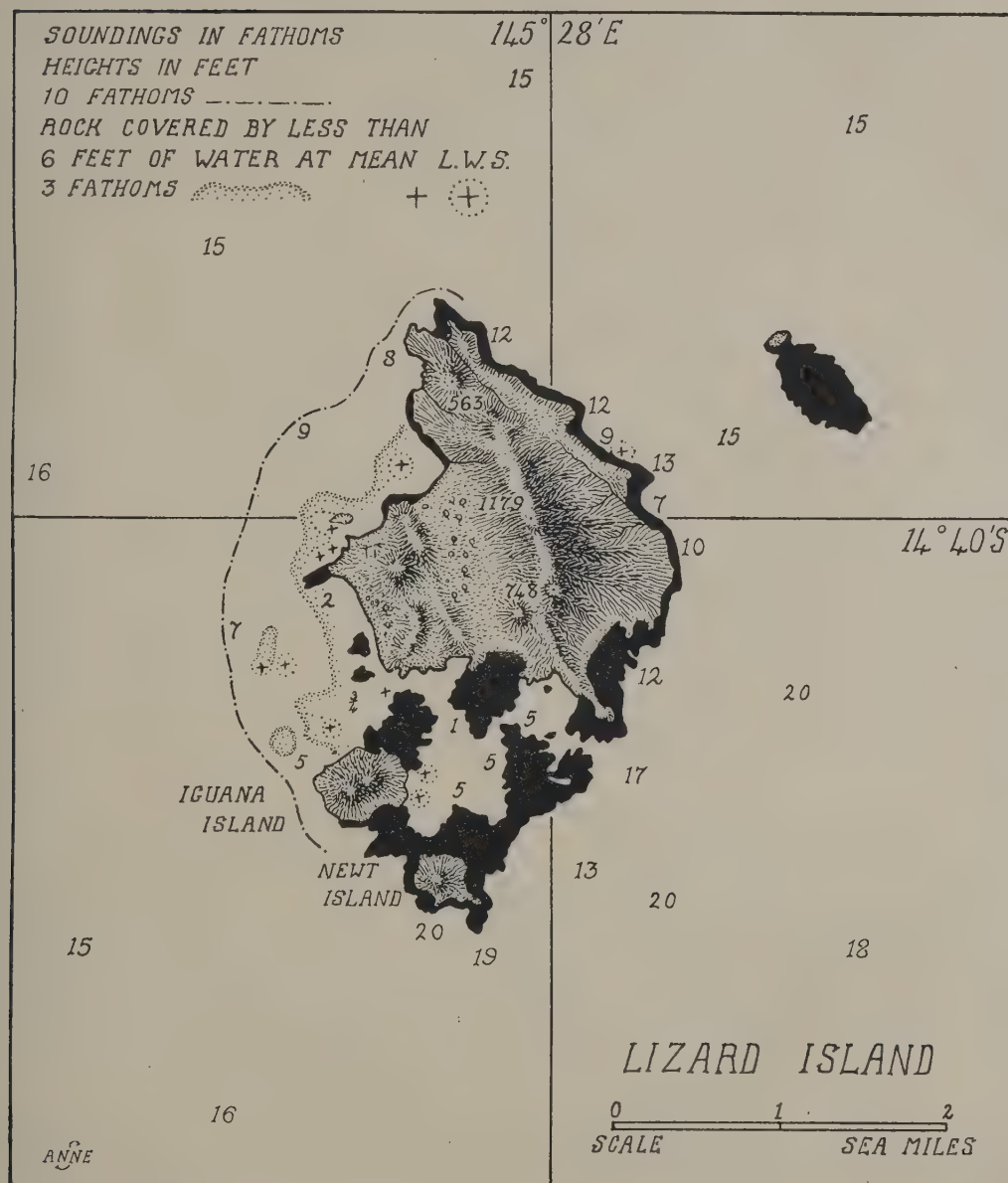
This ridge is not only lower, but also much narrower than the reef-crest. It is fairly continuous, but is interrupted here and there by somewhat wedge-shaped clefts. One may stand upon it at extreme low water, since the breakers curl up and over some few yards to seaward of it. From the ridge it is possible to see that the Pacific slope of the reef is at first gentle, perhaps for a few yards only, with an appearance as of the sudden descent into a chasm beyond.

4. THE INNER MOAT. (Plate XXIII, fig. 4.)

A second moat occurs immediately to westward of the reef crest and is about 50 yds. wide. It is less well defined than the outer moat, being intermittent and in places hardly recognizable, but is none the less a distinguishable zone. It is not more than 12 to 18 in. deep, often less.

5. THE BOULDER ZONE.

A belt bounding the inner moat along its western side and composed of boulders, coral fragments and shells, distributed in a haphazard manner.



TEXT-FIG. 6.—Modified from Admiralty Chart no. 2923. The principal reefs, or groups of reef-patches, about the island are represented in solid black. For description see p. 87.

6. THE INNER PARTS OF THE REEF. (Plate XXIV.)

From the outer ridge, going westward as far as the boulder zone, there is no large body of water present. Such water as exists is contained within the moats and in pools on the reef-crest and among the boulders. From the western edge of the boulder zone, still going westward, the substratum changes from rock to sand, and the sand is covered by water, continuous with that of the sea between the mainland and the Barrier. At first the sandy floor lies beneath water only a foot or two in depth, but it slopes gradually downward so that before long it has reached a fathom in depth, then 2 or 3 fathoms. By the time the western limit of the reef is reached, between the tips of its recurved horns, the water has become considerably deeper. From this sloping sandy floor there arise masses of coral rock of various forms and sizes, supporting a rich growth of living coral on their upper surfaces. Such of these masses as arise from 2 or 3 fathoms or more, mostly constitute curious table-like structures with precipitous or overhanging sides, and often many feet in diameter. The region in which these occur may be termed the *ZONE OF CORAL HEADS*, and this passes gradually, as the water shallows towards the boulder zone, into the *ANCHORAGE CORAL ZONE*, a region in which the height of the coral masses becomes less and less, and in which they form a labyrinth of intricate reefs with pools and channels between.

As the extremities of Yonge Reef are approached, some of the zones above defined disappear or become modified. The details of these changes are not relevant to the present account, and are described further on in the paper (p. 82). The structure of the recurved horns cannot be described, as we had no opportunity of examining them. Lastly, it should be noted that Yonge Reef is only accessible at low water of the lowest spring tides, and is not uncovered extensively many times in the year. As in the case of Batt Reef, the water floods the exposed parts rapidly after the turn of the tide.

E. LIZARD ISLAND. Lat. 14° 40' S. (Text-fig. 6.)

Lizard Island is a granite mountain 1179 ft. high, situated about 15 miles from the mainland, and 10 miles from the Outer Barrier. Upon this island we established a base from which we could visit Yonge Reef. The island is surrounded by fringing-reefs and curious patch-like reefs, unlike any of the types which we have so far described. We were unable to study these in any detail, but a note upon them will be found on p. 87.

THE ECOLOGY OF LOW ISLES.

(By T. A. and ANNE STEPHENSON and G. TANDY.)

The regions will be treated in the following order :

THE CAY.

THE REEF FLAT.

- A. THE MANGROVE SWAMP.
- B. THE FLAT APART FROM THE SWAMP.
- C. THE MOATS.
- D. THE MANGROVE PARK.
- E. THE ROCKY AREA.
- F. THE THALAMITA FLAT.
- G. THE SANDY AREAS.

THE RAMPARTS AND BOULDER TRACT.

- A. THE OUTER RAMPART.
- B. THE BOULDER TRACT.
- C. THE INNER RAMPART.

THE ANCHORAGE.

THE SEAWARD SLOPES OF THE REEF.

THE CAY.

(Plate IV, fig. 1 ; Plate V, figs. 1 and 2.)

The Cay itself is of little interest apart from the fact that it supports a dry-land flora and fauna. Its steeply sloping sides are submerged up to the vegetation line at high spring tides, and the most interesting items in their population are burrowing crabs and lamellibranchs. The swiftly running nocturnal crabs *Ocypode ceratophthalma* and *O. cordimana* make numerous burrows in the sand of the slope or on top of the cay ; and in a zone a little above the level of the flat, but well below the vegetation-line, there exists a large population, just beneath the surface, of a small smooth cockle, *Davila plana*.

The top of the Cay varies in level, but is roughly speaking flat. Large areas of it are carpeted by the large-flowered convolvulus *Ipomoea Pes-caprae* (Plate XXI, fig. 1), and this, round the fringe of the flat area in certain parts of its circumference, is associated with other creeping or low-growing plants (*e.g.* *Euphrobia eremophila* and *Vigna marina*), which together constitute a fairly conventional "*pes-caprae* association" of lesser vegetation. Apart from this ground-flora there are a number of deciduous trees of considerable size (*Terminalia Catappa*), some coconut palms (*Cocos nucifera*), and casuarinas (*C. equisetifolia*), in addition to which there are various bushes of lower growth, conspicuous among them the shiny-leaved evergreen *Scaevola Koenigii*. Climbing plants to be found among the bushes are the white-flowered *Passiflora foetida* and the dodder-like tangles of *Cassytha filiformis*, which latter tend to overgrow heavily the bush upon which they depend. Another notable shrub of more delicate growth is the white Jessamine, *Jasminum*

simplicifolium, and other bushes are *Tournefortia argentea*, *Vitex trifolia*, and *Premna obtusifolia*. The continuous occupation of the Cay by lighthouse-keepers for some years must have modified the original flora considerably.

As would be expected, a flora of this description carries with it associated insects and arachnids. The most prolific of these are ants, especially the small reddish-brown species *Pheidole variabilis*, which abounds everywhere. The larger insects are well represented by various grasshoppers (e. g. *Valanga irregularis*), by cockroaches (no doubt imported), beetles, butterflies and moths. The Lepidopteran fauna is considerable, but the majority of the species are night-flying forms attracted by the lighthouse. One species of Danaid butterfly (*Danaiida melissa* subspecies *hamata*), a pale blue and black form, was particularly noticeable at certain times when individuals, not in clouds, but as isolated fliers in considerable numbers, would be seen migrating from the mainland, many of them flying past Low Isles and out to sea. The Arachnida are represented by several species of spiders, some of them large, and by small scorpions (*Isometrus maculatus*) belonging to a species which has been introduced with shipping from the oriental region to the tropical and subtropical parts of Asia, Africa and America, as well as of Australia. Sand-flies were sometimes abundant at night on the slopes of the Cay, but there were only occasional mosquitoes. The ordinary "house-fly," *Musca domestica*, was common.

Beach Sandstone (Plate V, fig. 2; Plate XIV, fig. 1).—Surrounding the Cay on the lower part of its slopes are the various patches of "beach-rock" or "beach-sandstone," a rock formed by the cementing of the sand of the Cay by the deposition of calcium carbonate between the grains. The six patches of this rock are marked C1-6 on the key chart, and by far the largest of them is C6, the ridged structure of which is illustrated in Plate V, fig. 2. The exposed surfaces of this rock would appear to offer little attraction to organisms, but are extensively colonized none the less by a crust of blue-green algae, by lamellibranchs and gastropods, and to a lesser extent by *Enteromorpha*. The rock is often characterized, however, by the presence of sloping ledges with abrupt or overhanging shoreward margins, and these ledges, together with gullies in the rock and the spaces beneath isolated blocks, provide more protected and shaded crevices in which animals of less hardy disposition may shelter.

Notable amongst the exposed forms of the beach-sandstone is the rock-oyster *Ostrea mordax*, a sharp-edged form of a purplish colour which is gregarious and extremely abundant locally. This species is obliged to tolerate extremely high temperatures, since it inhabits a fairly high level, and is soon exposed by the receding tide, being left high and dry in the scorching sun for a very considerable proportion of its life. A. P. Orr took the temperatures of eight rock-oysters on 7th March, 1929 (not one of the hottest days), and the readings were 38.0°, 39.3°, 40.0°, 40.1°, 41.5°, 41.8°, 44.2°, and 44.8° C. (112.6° F.) respectively, the higher readings being in oysters slightly higher up the shore than the others. These readings are minimal. Still more remarkable is the fact that in the cracks between these oysters there are numerous specimens of a sea anemone (probably a species of *Anthopleura*), which have no protection from the sun beyond mucus and their contained water. *O. mordax* is also interesting in that, no doubt in correlation with its ability to withstand desiccation and high temperatures, it appears to occur principally in a rather strictly defined zone at a high level on the shore. This is well illustrated by fig. 4 on Plate V, where a large boulder is seen to be covered by a cap composed of scores of specimens of *O. mordax*, the lower edge of the cap being sharply

defined by the lower limit to which the oysters extend. The species is by no means restricted to the areas of beach-sandstone, occurring freely elsewhere on the reef wherever a suitable attachment such as a boulder or a mangrove-root is to be found at a proper level.

Noteworthy among the other organisms which inhabit the exposed parts of the sandstone are another oyster (*Chama jukesii*), a small periwinkle (*Planaxis sulcatus*), which occurs in great numbers in hollows and crevices at a high level, and a small species belonging to the Vermetidae. The large chiton *Acanthozostera gemmata* (Plate XXI, fig. 2), which attains a length of 6 in., and is one of the commonest inhabitants of the reef, may also be found exposed on the sand-rock, but this creature typically hides in a crevice as far as possible during the day, coming out freely on to the surface to feed at night. Acorn-barnacles and limpets are also present, but never in the profusion which they attain on many English coasts. Other animals seek the sheltered places habitually.

Two other species worthy of special mention are *Grapsus strigosus* and *Clibanarius virescens*. The former, a swift, long-legged crab with a striped greenish carapace, shelters deep in crevices at low water, but may be seen as the tide leaves or covers the rocks. The latter, a small hermit crab with yellow toes, may be found under detached pieces of rock, where it shelters in companies, some of which contain dozens of specimens, inhabiting shells of the most diverse of small gastropods.

The molluscan fauna of the sandstone, when studied in detail, reveals a succession of species which live in zones one above the other, and beyond these other species which occur without definite arrangement in zones. This zonation will be described in detail by T. Iredale elsewhere in this series of reports. The lower part of the stretch C6 is much attacked by boring lamellibranchs and sipunculids (see also p. 60); these are less prevalent on the small patches of rock to the south of the Cay.

THE REEF FLAT.

A. THE MANGROVE SWAMP.

(Plate V, fig. 1; Plate VI, figs. 1 and 2; Plate VII, figs. 1, 3 and 4.)

The several regions included under the general term "mangrove swamp" are diverse in nature and will be described successively; but regarded as a unit, the area has the characteristics of a tidal woodland of well-grown trees, containing glades of several types which are markedly sheltered from the wind and are quiet even on a windy day. The region has been colonized, not only by the dominant mangrove *Rhizophora*, but also by a series of plants and animals characteristic of mangrove swamps or of littoral areas, but not of coral reefs—forms which would normally be found on beaches or in estuaries or low-lying coastal areas on the mainland. Conversely, the swamp is invaded to a certain extent by corals and by other typical reef species.

The regions of the swamp will be considered for descriptive purposes under the following headings:

The Dense Woodland.

The Sandy Pools.

The Passages into the Swamp.

The Muddy Glades.

The Shingle Tongues.

THE DENSE WOODLAND. (Plate VII, fig. 3.)

We can say very little about this, because it is of thick growth and almost impenetrable. The trees are nearly all *Rhizophora mucronata*; they grow to a considerable size, their roots and the lower parts of their trunks are submerged at high water, and the ground beneath them consists of mud or muddy sand, often with shallow pools. There are a certain number of epiphytic lichens and fungi on their trunks and branches, and of epizoic sedentary animals on their roots. Snails of the genus *Melarhaphe* inhabit their leaves and branches, and crabs, hermits and fishes live among the roots, some of the former climbing the trees. Some of the trees are very old, and some are fine timber-trees with 50 or 60 ft. of clean bole.

THE SANDY POOLS. (Plate VII, fig. 4.)

The largest of these is the pool IM1 of the key chart, which occupies an elongate glade and which does not dry out at low water, but contains even then from a few inches to more than a foot of water. The bottom consists mainly of fairly firm sand, but becomes soft and muddy in places, and is often covered by thin black muddy deposits or by greenish scum. Cyanophyceae are ubiquitous and infest organic debris. Under the roots of mangroves are extensive carpets of the small film-fern-like alga *Caulerpa verticillata*, but the floor is free from *Thalassia*. On the living trees one finds *Melarhaphe*, and in the wood of dead ones a flourishing population of *Teredo* of more than one kind. Sponges* are a feature of the pond, some growing on the ground and others, together with compound ascidians, on mangrove roots, which are also colonized in places by a red-brown *Tubularia*-like hydroid (*Myrionema amboinense*). The fauna of the bottom includes both surface and burrowing species—crabs, hermits, cockles and other bivalves, prawns, tube-making Polychaetes, naticas, etc.† Species of particular interest are the heavy blue and green swimming-crab *Thalamita crenata*, which inhabits part of the mangrove area and also the mangrove park, but only exceptionally strays on to the open flat; the common dingy-coloured mangrove hermit *Clibanarius striolatus*, which abounds in shells of *Pyrasus* and *Telescopium*, and which is also plentiful in the mangrove park, close to the swamp; the cockles *Gafrarium pectinatum* and *G. tumidum*; and the surface-living *Holothuria scabra*.

Other pools somewhat similar to IM1, but much smaller, and offering little of special interest, are IM6 and IM7, the latter having a fairly firm bottom, the former a yielding floor of sand and mud.

There is, however, another small pool of a most interesting nature which may suitably be mentioned here. It lies between the inner rampart and the dense woodland, and is labelled RP3 on the key chart. The bottom here is sand, partly covered by *Thalassia*, and the pond is remarkable for its interesting fauna of coelenterates, clams and holothurians. *Pocillopora bulbosa* flourishes here, sometimes growing on mangrove roots, and other living corals are species of *Acropora*, *Montipora*, *Millepora* and massive *Porites*, and *Astraeids* of more than one genus. Zoanthids of two species are common; *Stoichactis kenti* is plentiful, and there is a densely gregarious colony consisting of scores of individuals of the extraordinary sea-anemone *Phyllodiscus cinctus*. This animal stings the fingers

* The following sponges occur here or in similar places: *Spirastrella purpurea*, *Chalina camerata*, *C. clathrata*, *Cladochalina pulvinatus*, *Gellius tocius*, *G. pumilus* and *Spongea digitata*.

† The term "natica" is used in this report in a somewhat wide sense, in the same way in which one speaks broadly of "chiton," and covers several species of the genera *Natica* and *Uber*.

quite badly, since in spite of its small size and delicate texture it is well supplied with large nematocysts; it also provides an example of a curious reaction to light. In specimens which were kept alive for a time, the tentacles, which are slender and pale bluish white, were usually kept partially or completely retracted in strong light, whereas the ruff of brown vesicles of complicated structure which occurs halfway down the body was widely expanded. In a dim light the reverse was the case. The clams found in the pool were *Hippopus hippopus*, *Tridacna crocea* and *T. fossor*. Four species of holothurians at least were present, including *H. argus*, *H. leucospilota* and *Synapta maculata*. This pond, together with the passages into the swamp next to be described, offer most curious examples of the presence of elements belonging to the true reef fauna and flora in the marginal and sandy parts of the swamp. The large pond IM1 exhibits this also, but in a lesser degree.

THE PASSAGES INTO THE SWAMP.

These passages deserve special mention, since they illustrate further the penetration of reef-animals into the woodland which has just been noted. The most perfectly developed of these passages are striking and curious features, consisting of a number of narrow, regular tunnels, free from trees and floored in the main by sand, which lead from the mangrove park into the pools inside the swamp. The adjacent tunnels P5-7 may be described as examples. Of these P5 is the most perfect, P6 nearly as well defined, P7 imperfect. They are channels, deep in parts, with a firm sandy floor grading locally into mud. In the entrances from the park there is *Thalassia* and *Halimeda*, and *Caulerpa verticillata* on or under mangrove roots. The water in the passages is inhabited by a small garfish, *Zenarchopterus dispar*, a species new to the Australian fauna. On roots flanking the passages, and on shells and dead coral among them, are small living colonies of massive *Porites* and *Cyphastrea*, of a species of *Leptastrea* and a peculiar species of *Porites*, the last especially being common. The most striking feature lies in the sponges, which are numerous and of several kinds. Compound Ascidians are also common, many of these and the sponges, together with oysters, living on roots. The Ascidians include a small pink species of *Didemnum* and the green *Diplosoma virens*. Noteworthy among the sponges is *Gellius toxius*, a soft, purplish-black form which trails along the roots and which has tall chimney-like tubes bearing the oscula. *Melarchaphe* and hermits, as usual, climb the trees. Conditions of life in these passages are affected by a distinct scour of water through them during the ebb and flow of the tide. A. P. Orr states that in one of the passages where he worked, except at slack water of high tides, there is a current of up to about 3 miles per hour or more.

THE MUDDY GLADES. (Plate VI, figs. 1 and 2; Plate XXVII.)

These are sinister places which might be a hundred miles from any coral reef for all the connection they appear to have with it. They are openings in the trees, floored by foul black mud on which lie whelks of unpleasant aspect by the score, amid dead tree-trunks riddled by *Teredo*; their floors are exposed at low water, leaving only shallow pools here and there. The fauna is distinctive. The whelks (Plate VI, fig. 2), black creatures with dingy pyramidal shells, are *Telescopium telescopium* and *Pyrazus palustris*. These form one of the most marked characteristics of the mud-glades, although

they occur elsewhere in the swamp. Their shells are common in the sandy pools and peripheral regions, but are there usually tenanted by *Clibanarius striolatus*. Another abundant inhabitant of the mud-glades is the skipping fish *Periophthalmus koelreuteri*, in addition to which are the burrowing red Crustacean *Thalassina anomala*, numerous crabs which also burrow in the mud, and small gastropods. The large black lamellibranch, *Cyrena coaxans*, is also to be found (this being sometimes used for food by native crews, if one may judge from the existence of a pile of empty shells on one of the shingle tongues), and even in this black mud there are naticas. On the shells of *Telescopium* and *Pyrarzus* may be found oysters (e. g. *O. mordax*). The black mud, although one sinks into it knee-deep, is actually a superficial layer, as has been demonstrated by the boring described in another report by A. P. Orr (Vol. I, No. 5, p. 117); the mud appears to be *superimposed upon the reef flat*. The glades above described are those marked IM2, IM4 and IM5 on the key chart. They vary a little individually, but the description given applies in general to all of them. The mangrove *Bruguiera Rheedii* occurs in places along their margins.

THE SHINGLE TONGUES. (Plate VII, fig. 1; Plate XXVII.)

These are regions of coral shingle inside the mangrove area, which are covered for the most part at high water of tides rising about 7 ft. above datum. So far as we can judge, they appear to antedate the mangroves. As the two tongues are rather different, they will be described separately.

IM4B is a large L-shaped area of shingle, which is limited on its seaward side by the inner rampart, and flanked along the greater part of its other edges by the mud-glades IM4 and IM5. It forms dry land at low water, and consists of dirty shingle, loose on top, but fairly compact and mixed with sand and mud below. In places the shingle is much infested by blackish rust-like Cyanophyceae, and supports patches of the fleshy creeping plant *Sesuvium Portulacastrum* (a form reminiscent of *Mesembryanthemum*, Plate XIX, fig. 3), and in addition to this a grass and other low-growing plants. The fauna is interesting, consisting of isopods (probably of more than one species, including *Ligia australiensis*), some of which move extremely rapidly; of small scuttling crabs; of numerous small gastropods of several kinds, many of them under the shingle; of black and green ants (including *Oecophylla smaragdina* subspecies *virescens*, and *Polyrhachis sokolova*), and of butterflies, sand-flies and other small flies. There are also geckos and, perhaps most curious of all, earthworms (*Pontodrilus bermudensis*) are to be found in the mud beneath the shingle. This area is also characterized by the presence of a number of enormous pits, a foot or more in diameter, excavated in the shingle by the large blue mangrove crab *Scylla serrata*. At the bottom of the pit, which is inclined at an angle, there is sometimes standing water, in which the crab may be seen. At Low Isles these burrows occur mostly on this one spot, but are found occasionally on the Long Tongue and the inner rampart. This habit of digging in shingle is apparently an exceptional one for the species, which is a well-known mangrove crab of the Australian coast, but normally burrows in mud.

On the surface of this shingle area there are two small banks higher in level than the rest (Green Ant Island and IM4A), which must constitute dry land even at high water, at ordinary tides. Green Ant Island (Plate VII, fig. 1) is a remarkable spot, composed of fine-grained clean shingle and sand, contrasting sharply with the coarse, dirty shingle of the greater part of the tongue, and supporting a dense thicket of characteristic dry-land scrub, of the type which colonizes a mainland strand. The flora of flowering plants on

these few square yards is considerable, and notable among them are the tree *Thespesia populnea*, the scandent *Flagellaria indica*, the blue-flowering herb *Commelina cyanea*, the grass *Lepturus repens*, and *Achyranthes aspera*. These species most of them occur on Green Ant Island only. The green ant, *Oecophylla smaragdina*, swarms all over this vegetation. The mound IM4A is similar to Green Ant Island, but its flora contains fewer species, among which are *Thespesia populnea* and the Milky Mangrove *Excoecaria agallocha*.

The other shingle area, the Long Tongue of the chart, is an elongated ridge considerably overgrown by trees, and merging at its edges into dense woodland on one side, and into the mud-glade IM2 on the other. At its northern extremity it meets an area consisting of patches of soft muddy gravel grading into swamp, but the ridge proper constitutes, at low water, a corridor of firm land through the trees, made of coral shingle knit together by sand and mud. The soft northern area is honeycombed by the burrows of various crabs, notably *Gelasimus dussumieri*, the males of which have one enormously developed chela, and are brilliantly coloured in cobalt blue, white and orange, whilst the females lack the large claw and are dark greenish in colour. The mangrove whelks occur in this region. The dry part of the tongue also contains many crab-burrows, and has a fauna of black and green ants, small gastropods, isopods and earthworms, as in the case of IM4B. At one side of the tongue is a small area of fine white shingle, *Sesuvium* and bushes, similar to IM4A. The large brilliant green and black butterfly *Troides priamus* subspecies *euphorion* was seen in this region. Organisms characteristic of the shingle-tongues (though not necessarily confined to them) are indicated by asterisks in the list on p. 42.

ANALYSIS OF THE FAUNA AND FLORA OF THE MANGROVE AREA.

The fauna and flora of the mangrove area as a whole, therefore, include several types of plant and animal community. The species overrun each other's territory to a certain extent, but the distinction into groups is none the less apparent. The fauna and flora may be analysed as follows:—

I. The principal animal communities are three in number :

1. The characteristic inhabitants of the muddy glades.
2. Those of the shingle tongues, which include dry-land and littoral forms.
3. Those of the sandy pools and passages, where reef and mangrove fauna intermingle, but where only certain members of the reef fauna penetrate.

II. The flora is differentiated into three series :

1. *Rhizophora* and its associates.
2. *Sesuvium* and other low-growing forms.
3. A dry-land flora, including species which may occur elsewhere in situations unconnected with shore or mangroves, sometimes at high levels.

III. The following points are also relevant :

1. The mangrove area includes species which are limited to it or which do not stray far beyond it. Such are *Pyrazus*, *Telescopium*, *Thalassina*, *Scylla*, *Clibanarius striolatus* and *Periophthalmus*.
2. It includes also, particularly on the shingle tongues, species which may occur on the mainland apart from mangrove areas—*e. g.* ants, geckos, flowering plants, earthworms, and some of the gastropods. Even *Periophthalmus* is sometimes a littoral form unconnected with mangroves,

3. Forms such as *Metopograpsus messor* are equally characteristic of the mangrove area and the ramparts. Crabs of the genus *Gelasimus* are plentiful in certain places outside the swamp as well as inside it.
4. The list given below does not include the corals, sponges, ascidians, holothurians, hydroids and anemones, which clearly belong to the reef-fauna proper.

The Low Isles mangrove area, therefore, shelters a number of forms, whether littoral or palustrine, which would not occur on a coral reef pure and simple—that is to say, on one such as Batt Reef or a member of the Outer Barrier series, where nothing is exposed at high water. Many of the swamp animals are species modified for aerial respiration, and some of the plants have accessory breathing organs connected with the immersion of their roots in mud.

SPECIES CHARACTERISTIC OF THE MANGROVE AREA.

(Asterisks indicate organisms characteristic of the shingle tongues, though not necessarily confined to them.)

ANIMALS.

OLIGOCHAETA.

- **Pontodrilus bermudensis*.

ISOPODA.

- **Igla australiensis*.

ANOMURA.

- Thalassina anomala*.
- Clibanarius striolatus*.

BRACHYURA.

- **Scylla serrata*.
- Thalamita crenata*.
- Sesarma bidens*.
- „ *villosa*.
- Euplax tridentatus*.
- **Metopograpsus messor*.
- Gelasimus annulipes*.
- „ *dussumieri*.

INSECTA.

- **Oecophylla smaragdina*.
- **Polyrhachis sokolova*.
- Sand-flies and mosquitoes.

GASTROPODA.

- Nerita lineata*.
- „ *planospira*.
- * „ *plicata*.
- * „ *striata*.

PHANEROGAMS.

- **Commelina cyanea*.
- **Achyranthes aspera*.
- **Lepturus repens*.
- **Excoecaria agallocha*.
- **Avicennia officinalis*.
- **Thespesia populnea*.
- Rhizophora mucronata*.
- Bruguiera Rheedii*.

GASTROPODA—continued.

- **Bembicium melanostoma*.
- **Melarhaphes scabra*.
- * „ *undulata*.
- Pythia nux*.
- **Melampus adamsianus*.
- * „ *granifer*.
- **Quoyia decollata*.
- Pyrasus palustris*.
- Telescopium telescopium*.
- **Cerithium patulum*.
- Naticidae*.

LAMELLIBRANCHIA.

- Ostrea mordax*.
- Gafrarium pectinatum*.
- „ *tumidum*.
- Tellina palatam*.
- „ *remies*.
- Cyrena coaxans*.
- Teredo*.

PISCES.

- Periophthalmus koelreuteri*.
- var. *argenteolineatus*.

REPTILIA.

- **Geckos*.

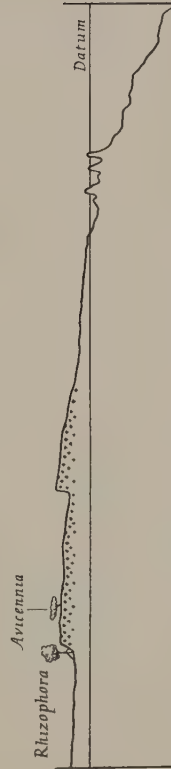
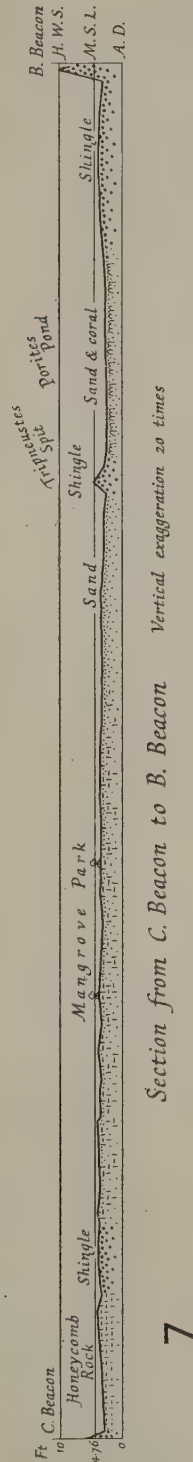
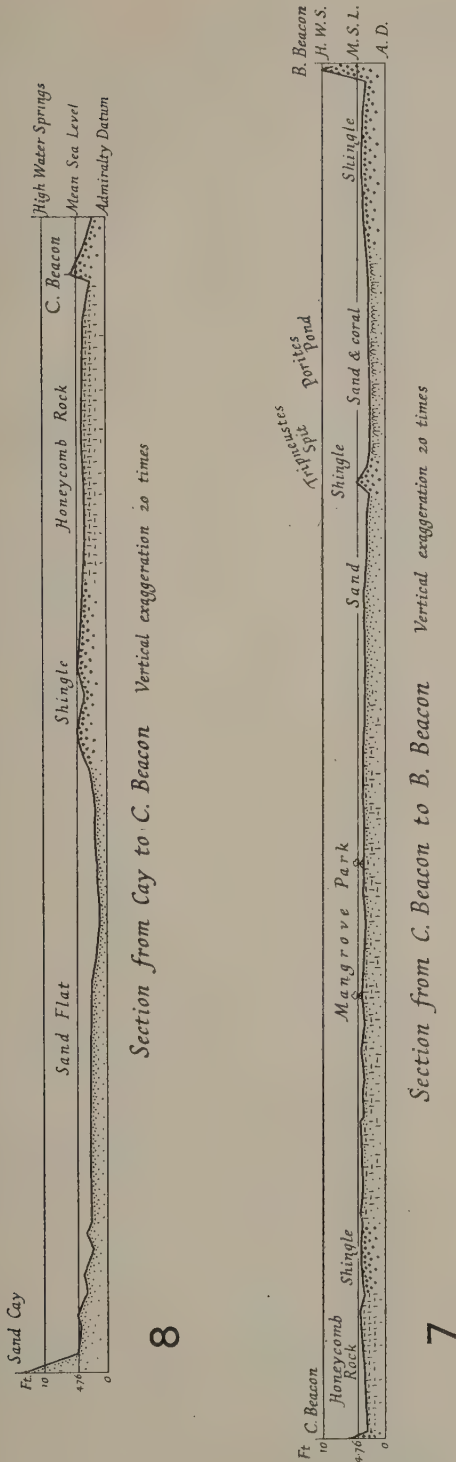
PLANTS.

PHANEROGAMS—continued.

- Ceriops tagal*.
- **Sesuvium Portulacastrum*.
- **Flagellaria indica*.

CRYPTOGAMS.

- Caulerpa verticillata*.
- **Cyanophyceae*.
- Lichens*.
- Fungi*.



TEXT-FIG. 7.—Sections across the Low Isles flat, and across the ramparts. The positions of these sections on the reef are indicated in Text-fig. 11. Note the difference in height between the eastern part of the flat (about 4 ft. above datum) and of the western part (2.2 to 2.5 ft.); section 9 in Text-fig. 11 (not illustrated here) amplifies the information represented here, giving heights of 2.5–3.2 ft. across the flat. The number beside each section corresponds to a number in Text-fig. 11.

B. THE FLAT APART FROM THE SWAMP.

It will be advisable before describing the several parts in detail to consider the reef-flat in general, as distinct from the mangrove area, which forms a very special part of it.

The following is a list of organisms which may be regarded as typical reef-flat species. If we consider the flat as comprising three principal regions—the moats, the mangrove park, and the western part (including Thalamita flat, Sand flat, and adjacent areas)—the great majority of these organisms occur in all three regions. This does not mean that some of them are not more abundant on one part of the flat than another, nor that given species are not specially characteristic of particular areas; but it provides an indication of the range of life on the flat, on the basis of which the differentiations may afterwards be considered. Sand-dwelling animals are listed separately on p. 56.

SPECIES CHARACTERISTIC OF THE REEF FLAT.

ANIMALS.

FORAMINIFERA.

Orbitolites complanata.

PORIFERA.

Cinachyra australiensis.

Gellius fibulatus.

„ *sagittarius*.

Clathria aculeata.

Spirastrella purpurea.

Euspongia irregularis.
var. *pertusa*.

HYDROZOA.

Myrionema amboinense.

Dynamena crisioides.

ZOANTHINARIA.

More than one common species.

ACTINIARIA.

Stoichactis kenti.

Actinodendron plumosum.

MADREPORARIA.

Pocillopora bulbosa.

Leptastrea.

Galaxea.

Favia.

Montipora ramosa.

Acropora hebes.

Porites (massive forms).

POLYCHAETA.

Eurythoe complanata.

Iphione muricata.

Spirobranchus giganteus.

SIPUNCULOIDEA.

Boring species.

CIRRIPEDIA.

Acorn barnacles.

NATANTIA.

Crangon strenuus.

„ *ventrosus*.

ANOMURA.

Clibanarius virescens.

Dardanus megistos.

BRACHYURA.

Calappa hepatica.

Thalamita admete.

„ *stimpsonii*.

Actaea hirsutimana.

Atergatis ocyroe.

Phymodius unguatus.

Pilumnus vespertilio.

STOMATOPODA.

Gonodactylus chiragra.

AMPHINEURA.

Schizochiton incisus.

Acanthozostera gemmata.

GASTROPODA.

Trochus fenestratus.

„ *niloticus*.

Vermetidae.

Cypraea annulus.

„ *errones*.

„ *moneta*.

Strombus luhuanus.

Pterocera crocata.

Melo diadema.

Siphonaria denticulata.

Onchidium.

ANIMALS—*continued*.

LAMELLIBRANCHIA.

Ostrea cerata.
 „ *crista-galli*.
 „ *mordax*.
Spondylus ducalis.
Lima tenera.
Pinctada margaritifera.
Isognoma isognomum.
Modiolus auriculatus.
 Boring species (*Lithophaga*, etc.).
Arca fusca.
Tridacna crocea.
 „ *fossor*.
Hippopus hippopus.
Chama jukesii.

ASTEROIDEA.

Linckia laevigata.
Nardoa pauciforis.
Culcita novae-guineae.

ECHINOIDEA.

Echinometra mathaei.
Tripneustes gratilla.
Centrechinus setosus.

OPHIUROIDEA.

Ophiothrix longipeda.
Ophiocoma scolopendrina.
Ophiarthrum elegans.

HOLOTHUROIDEA.

Synapta maculata.
Stichopus chloronotus.
Holothuria atra.
 „ *coluber*.
 „ *leucospilota*.

ASCIDIACEA.

Didemnum candidum.
Diplosoma virens.

PLANTS.

PHANEROGAMS.

Rhizophora mucronata.
Halophila ovalis.
Thalassia Hemprichii.

PHAEOPHYCEAE.

Sargassum lanceolatum.
 „ *latifolium*.
 „ *torvum*.
Turbinaria turbinata.
Hydroclathrus clathratus.
Cystophyllum muricatum.
Dictyota Bartayresiana.
 „ *ciliata*.
Padina australis.
 „ *Commersonii*.

CHLOROPHYCEAE.

Caulerpa peltata.
 „ *racemosa*.
Halimeda cuneata.
 „ *Opuntia*.

CHLOROPHYCEAE—*continued*.

Bornetella nitida.
Dictyosphaeria favulosa.
 „ *sericea*.
 „ *Versluysii*.
Boodlea paradoxa.

FLORIDEAE.

Laurencia botryoides.
 „ *papillosa*.
Acanthophora spicifera.
Spyridia filamentosa.
Digenea simplex.
Amphiroa fragilissima.
Melobesia (encrusting forms).

CYANOPHYCEAE.

Species of the group very prevalent,
 including—
Lyngbya majuscula and
Hormothamnium solutum.

C. THE MOATS. (Plate VIII, figs. 2 and 3 ; Plate IX, figs. 1, 3 and 4, etc.)

CONDITIONS OF LIFE IN THE MOATS.

The conditions which prevail in the moats are clearly of a special nature, and will determine somewhat strictly the range of life which can flourish there. Any organism attempting to establish itself will be subject to the following circumstances :

1. The water is shallow, and is still during much of the period of low water.

2. The temperature during this time therefore becomes very high in hot, calm weather, and may exceed 35°C . (95°F .), though probably rarely, if ever, reaching 40°C .

3. The organisms not living in protected positions are exposed to very strong illumination.

4. During the wet season a heavy fall of rain during the period of low water may cause a sudden change of salinity, which will not be rectified until the tide covers the flat. We can record a range only of $35^{\circ}/_{\infty}$ to $27^{\circ}/_{\infty}$; but undoubtedly the salinity sometimes falls considerably lower than $27^{\circ}/_{\infty}$; for a pool 12 cm. deep with little growing coral, we have a record of $17.1^{\circ}/_{\infty}$.

5. During the ebb and flow of the tide a distinct series of currents is set up in the moats, since the water drains away through the gaps in the rampart and boulder tract, after the main volume of it has left the flat, and enters again through these before it submerges the flat as a whole.

6. A considerable to-and-fro movement of sediment appears to take place in the moats as a result of the currents just mentioned. The actual amount of fresh deposition taking place is probably low.

7. At the end of the period of low water, during the daytime, the oxygen-saturation of the water is very high, and may reach 270%. At the end of low water at night, however, it may fall as low as 20%, and in the event of an occurrence such as a serious visitation of *Trichodesmium*, the oxygen-content may become reduced to zero or very near it, even during the day.

Conditions of life on other parts of the flat will represent modifications of this state of affairs, varying according to situation, nature of substratum and depth of the pools isolated at low water.

THE WESTERN, MIDDLE, FUNGIA AND MADREPORE MOATS.

This principal stretch of moat is above all that region of the flat in which coral growth predominates. It is a continuous pool of winding form, lying just inside the western part of the rampart and boulder tract; it is a foot deep or rather more in its deeper parts, and gradually becomes shallower towards the Thalamita flat. This shallow side, indeed, is often rather distinct from the rest, since long trailers of bladder-wrack (*Cystophyllum* and *Sargassum*) are plentiful here, and the growth of branching corals relatively sparse.

Coral Platforms (Plate VIII, figs. 3 and 4; Plate IX, fig. 1).—In the seaward part, however, *Montipora ramosa*, *Acropora hebes* and massive *Porites* are in the ascendant, and between them occupy a high proportion of the available space. These corals exhibit a curious development connected with the shallowness of the water. They grow in a normal fashion until their tops project above the level of low water; they may then survive with projecting tips for a longer or shorter period; but sooner or later the projecting parts are killed, become infested by microphytic algae and sediment, and encrusted by nullipores (*Melobesieae*)*; so that ultimately the coral colonies are converted into flat-topped platforms, dead across the top and alive around the edges. This process may affect individual colonies or, if the growth has been dense so that fields of branching colonies have been formed, it may convert a whole field into a platform. The general

* The group of calcareous algae which includes *Lithothamnion* and related genera.

result of this is to create a bewildering maze of level platforms with pools between. Three of our figures illustrate this process. In Plate IX, fig. 1, may be seen (on the left) a tuft of *Montipora ramosa* which is as yet alive on top; to the right is another tuft in which the death and flattening of the top has begun. Plate X, fig. 4, gives a detailed view of the top of a platform in an advanced stage of formation, and shows the overgrowth of nullipores and the general incrustation of the surface. Plate VIII, fig. 3, shows the general appearance of the moat close to the gap C, where *Acropora hebes* predominates; and in this case the platforms are not yet dead on the top. The extent and composition of the platforms varies in different parts of the moat; massive *Porites* becomes converted into platforms as readily as the branched species, though the details are a little different. Astreaid corals, especially species of *Favia*,* are common among the platform-building forms (Plate IX, figs. 3 and 4), and these also often develop dead flattened tops.

Inhabitants of the Platforms (Plate X, figs. 1, 3 and 4).—The interstices of the coral platforms offer a home to innumerable commensal, boring and shelter-loving forms of life, the more or less concealed fauna and flora being rich in species as well as in individuals. The urchin *Echinometra mathaei* (Plate X, fig. 3) is common, and there are anemones of a number of species, besides various crabs and prawns. Nullipores are usually well developed and richly coloured on shaded surfaces.

The commensal crabs, prawns and fishes which are found on living coral and anemones may suitably be mentioned here, since they are abundant in the moats as well as in certain other places. Several of the common anemones harbour fish, prawns or both; we have not seen these commensals enter the coelenteron of the polyp, but they shelter freely among the tentacles. Commensal fish and crustacea are widespread among the living coral, different species of coral often having particular commensals, which are usually so coloured that they tone with the coral or contrast suitably with it. A dull reddish madrepor, for instance, may shelter a colony of small fish, sometimes brilliant green in colour, sometimes bright yellow. One of the dominant corals of the moats is *Pocillopora bulbosa*, a yellowish brown branching form which commonly shelters the red and purplish crab *Trapezia cymodoce*.†

General Population of the Moats (Plate IX, figs. 3 and 4; Plates X, fig. 2; Plate XVIII, figs. 1-4; Plate XX, fig. 2).—Among the platforms and in the pools between them are to be found a number of other animals, and among these the clams are important. The Low Isles moat supported several specimens of the giant species *Tridacna derasa* (Plate XVIII, fig. 2). The smaller species, *T. crocea* and *T. fossor* are very abundant, and these are extremely conspicuous because of the extraordinary range of brilliant colours and patterns exhibited by the exposed edges of their mantles.

* The generic name *Favia* is used in this report in a broad sense, as covering the species sometimes grouped under *Favia*, *Favites*, *Acanthastrea* and *Goniastrea*. It is a matter for discussion whether or no these groups should be regarded as valid genera, but for ecological purposes they may be suitably included under *Favia*.

† Some further details are as follows: Less common commensals of *Pocillopora bulbosa* are the crabs *Actaea polyacantha* and *Cymo andreossyi*, and a species of *Periclimenes* (a prawn). The large anemone *Stoichactis kenti* and the crevice-dwelling anemone *Thalassianthus hypnoides* often shelter the prawn *Periclimenes brevicarpalis*. A similar if not identical prawn lives with the actinians *Actinodendron plumosum*, *Cryptodendron adhaesivum*, and *Thalassianthus hemprichii*. *S. kenti* often provides a home for small fish, *Amphiprion bicinctus* and *Actinicola percula*. Some crevice-haunting species of the platforms are the crabs *Atergatis ocyroe* (very common), *Eriphia sebana* and *Pilumnus spinicarpus*: the prawn *Periclimenes spiniferus*; and soft corals of the genera *Rhodactis* and *Actinotryx*.

The colours range from deep peacock blue or violet, through a variety of shades of brilliant green and paler blue to purple and gold, brown and yellow, and so forth. In the case of *T. fossor* almost any pattern imaginable may be found in one specimen or another; but in spite of this variability, it does not produce quite the same series of patterns as do the other species mentioned. Another very common clam, *Hippopus hippopus*, introduces variations upon a duller set of colours; and the rarer *T. squamosa* produces yet another kind of pattern. Two mantles with completely different patterns, though probably both belonging to the same species, are illustrated in Plate XVIII, figs. 3 and 4; and other examples, from different species, may be seen in Plate XVIII, figs. 1 and 2.

Echinoderms are a feature of the moat, among them the brilliant blue starfish *Linckia laevigata* (Plate X, fig. 2), and the holothurians *Stichopus chloronotus*, *Holothuria leucospilota* and *H. coluber*. Isolated individuals of the long-spined urchin *Centrechinus (Diadema) setosus* are fairly common, and sometimes colonies of them (Plate XX, fig. 2) are found, which may remain in approximately the same situation for months at a time. A straggling branched sponge, green in colour, is of frequent occurrence and rapid growth; this form is actually a combination of a sponge (*Gellius fibulatus*) with an alga. Another sponge, bright magenta in colour (*G. sagittarius*), is conspicuous, at least at certain times of year; it has curious flower-like crowns, which frequently become detached and float away on the water. The living coral, especially the massive forms of *Porites*, is much colonized by the tube-dwelling polychaete *Spirobranchus giganteus*, which expands fans of deep blue, scarlet, and other colours at the surface.

The algae of the moats are abundant. Some of them make turf-like tangles amongst the platforms, often overgrowing the coral to a considerable extent, or carpeting areas of dead rocky substratum. These forms include the bright green sponge-like masses of *Boodlea paradoxa*, and several species of "red" algae, which in this case are usually brownish or yellow-green in colour.* Apart from forms of low or mossy growth, there are several characteristic species of brown algae which attain a larger size. *Turbinaria turbinata* is one of these, and this species is a typical moat-dwelling form, whereas *T. ornata*, which is plentiful outside the rampart, is relatively infrequent inside it. The tufts of *Padina australis* and *P. Commersonii* are ubiquitous, neither species being restricted, apparently, to a particular habitat. The calcareous alga *Halimeda opuntia* is plentiful in the platforms; *H. cuneata*, which is less common, appears to prefer bare sand. Species of *Caulerpa* creep over coral blocks, and species of *Dictyosphaeria* are common on surfaces where they are exposed to very strong illumination and become bleached and powdery-looking in consequence.

The shells of clams, especially those of *Hippopus*, offer a foundation for a complicated fauna and flora of their own, and are extensively bored into from outside by various organisms, including a filamentous alga which makes the inside of the shell green.

The sandy floor of the moat is rarely free from *Thalassia Hemprichii*, but this is usually of relatively sparse growth and does not form a dense turf like that of the mangrove park. Its leaves, here as elsewhere, may be heavily colonized by epiphytes and epizoa.† Occasional seedlings of *Rhizophora* take root in the moats, but do not survive.

* *Acanthophora spicifera*, *Digenea simplex*, *Laurencia papillosa*, *L. botryoides*, etc.

† The epiphytes of *Thalassia* include species of *Ectocarpus* and *Polysiphonia*. *Valonia Forbesii* is a common epiphyte of the red alga *Digenea simplex*. Frequent epizoa are the ascidian *Diplosoma virens* and the foraminiferan *Orbitolites complanata*.

INDIVIDUAL CHARACTERISTICS OF PARTICULAR MOATS.

(1) *The Western Moat*.—The special feature here is that a very considerable number of coral species are represented, although many of them must be regarded rather as occasional intruders which have managed to survive, than as forms which are really suited to the locality. Beyond the species already mentioned, certain others are fairly common, and the total number of genera represented is at least fifteen.

(2) *The Middle Moat*.—That part of the Middle and Western moats which lies next to Asterina spit is largely occupied by a rocky platform, partly exposed at low water, on which the turf of *Boodlea*, *Hydroclathrus* and other algae is particularly well developed, and in parts of which the coral *Psammocora* is common. This latter form is almost confined, on the flat, to several regions near Asterina spit.

(3) *The Fungia Moat*.—This was named "Fungia moat" because it was characterized by the presence, amongst the dead branched coral which chokes up a good deal of it, of a large colony of *Fungia*. Three species at least were represented, of which one (a small night-flowering form) was very common, a much larger one which expands its tentacles during the day being less plentiful. The attached young of these species, in various stages of development, were abundant in the shelter of the dead coral.

(4) *The Madrepora Moat*.—A stretch containing a very healthy growth of coral, but of rather fewer species than in other parts.

(5) *The Northern and North-East Moats*.—These represent somewhat pale reflections of the principal moats already described. In the Northern moat species of *Galaxaura* are abundant, and there is a certain amount of immigration of animal species from the Anchorage. A small patch of the grass-like *Diplanthera uninervis*, found nowhere else on the reef, occurred here. In certain runnels (between Clam Spit and the Cay; between Tripneustes Spit and the Shingle Mound) there was a turf consisting of an almost pure growth of *Hydroclathrus clathratus*. This began to disappear in February, 1929. In the north-east moat the coralline *Amphiroa fragilissima*, which is ubiquitous in the moats, attains an abundance not paralleled elsewhere.

(6) *The Discontinuous Moat-pools*.—The series of discontinuous pools which lie inside the escarpment of the outer rampart, starting at the pool M1 of the key chart, and going round in an anti-clockwise direction as far as the pool M13, have been classed as a matter of convenience with the moats. They are, however, of a rather different nature. The large pool M7 is distinguished from the rest of the series because it has an arm which penetrates the mangrove swamp. It has a fairly typical moat population, and is peculiar in the possession of a special richness of *Stoichactis kenti*, of small Zoanthids which in places form a yielding carpet yards in extent, and in the existence of a few healthy colonies of fleshy alcyonaria (which occur here and there in moats, but are not among the characteristic forms) close to the mangroves. It includes also organisms characteristic of the mangrove park (e.g. *Myrionema amboinense*), and at the northern and southern ends of its seaward portion resembles the other pools in the series. Apart from this pool, the others have a more or less rocky floor, which, in the more western ones consists partly of honeycomb-rock (see p. 52 and Text-fig. 8), in the more easterly of inner rampart material. These pools vary individually, but are shallow and contain little or no living coral, the most noteworthy organisms being *Hippopus*, *Gellius fibulatus*, *Ophiocoma scolopendrina*,

Cypraea annulus, holothurians (*H. atra*, *H. leucospilota*, etc.), *Pilumnus vespertilio*, *Onchidium*, *Stoichactis kenti*, and turfs of algae (*Dictyosphaeria*, *Laurencia*, *Caulerpa*, *Halimeda*, etc.).

(7) *Porites Pond*.—The pool thus labelled on the chart is an isolated piece of moat of considerable depth in its northern and western part, shallowing to eastward and southward. It has a flourishing population of coral, amongst which massive *Porites* of large size is dominant; and supports a typical population of moat animals.

D. THE MANGROVE PARK.

(Plate VII, fig. 2; Plate XIII, fig. 4; Plate XIX, fig. 1.)

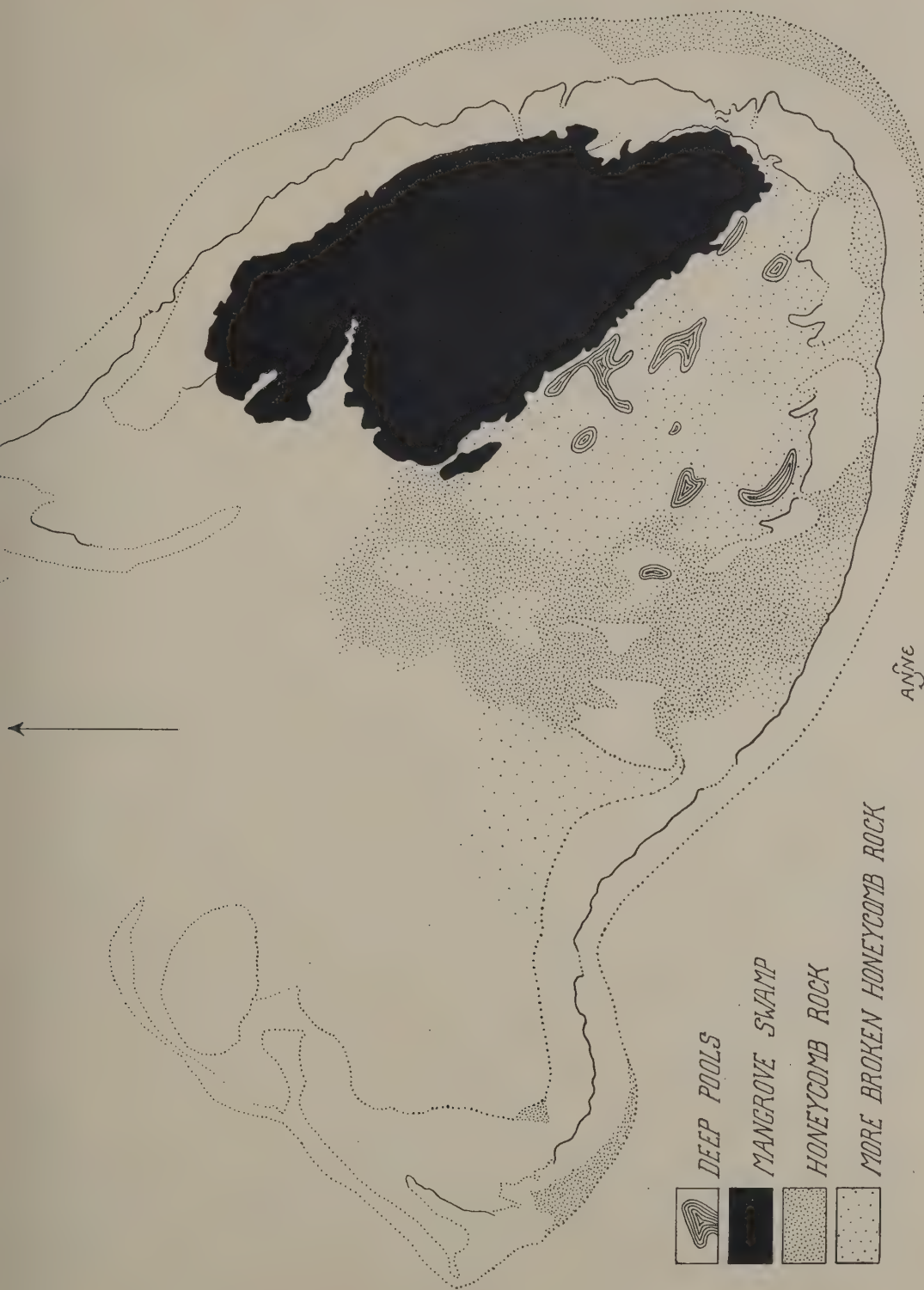
The mangrove park covers a large area, and its floor varies considerably both in nature and in level from one part to another. The "park" comprises approximately that part of the flat which is more or less successfully colonized by outlying trees or saplings of *Rhizophora mucronata* with their remarkably developed stilt-roots. Some idea of its nature may be gained from Plate XIII, fig. 4, but one cannot show in a photograph the other feature which characterizes the region, the greensward beneath the water due to the rich growth of *Thalassia Hemprichii*. A figure illustrating a patch of such turf in a thin place, heavily colonized by the macroscopic foraminiferan *Orbitolites complanata*, is given on Plate XIX, fig. 1.

The fauna and flora of the park vary somewhat from place to place, according to whether the substratum is sandy or rocky, and according to whether it is exposed at low water or lies in a shallow or deeper pool. On the coloured map of Low Isles the depths of the various parts of the park are indicated, and in Text-fig. 8 the relation between the deeper parts (which are sandy in the main) and the more rocky areas is shown. We shall not attempt to describe the rather subtle variations in the series of organisms which present themselves as one passes from rock to sand, from exposed regions to pools, from shallow to deeper water, since this would introduce too many complications. If the illustrations are studied carefully, however, in the light of the paragraphs which follow, a sufficiently clear idea of the variation to be expected should be acquired. The sections of the paper which deal with the rocky area of the flat, the *Thalamita* flat, and the sandy regions, also apply in part to the mangrove park.

The fauna of the mangrove park is not easily characterized. It includes many typical reef flat forms, and shares some species with the mangrove area; it contains a scattered population of living coral, but very much less than the moats; and it has a certain distinction of its own, being the headquarters of some at least of the inhabitants of the reef flat.

Corals recorded from the mangrove park are *Pocillopora bulbosa*, massive *Porites*, *Favia*, *Leptastrea*, *Cyphastrea* and *Heliopora*. They are nowhere abundant, and although there are deep and extensive pools they have no tendency to flourish as in the moats.

Near the mangrove swamp occur some curious areas of bare sand, where the water is rather deep, and there is little or no *Thalassia*, and on one of these a few specimens of the curious jellyfish *Cassiopaea andromeda* were found. This animal lies on its back, unless disturbed, with the fern-like oral arms outspread, so that it looks very like a specimen of the anemone *Actinodendron plumosum*, which is a common inhabitant of sandy places. In an area at Hope Isles comparable to the mangrove park this jellyfish was very common, and there was also a considerable amount of *Heliopora* in the form of platforms.



TEXT-FIG. 8.—To illustrate the distribution of "honeycomb rock" on Low Isles, and the relationship between the deeper pools and the rocky areas in the mangrove park. The conditions are represented only approximately. In the mangrove park the deeper sandy pools alternate in the main with the more rocky areas, suggesting the possibility that the former may be the result of the action of solvents (including mangrove mud during an earlier, more extended phase of the mangrove swamp ?) on a substratum once more uniformly rocky.

The epiphytes and epizoa of the mangrove roots are interesting. Among the former are *Valonia aegagropila*, and a remarkable form of *Turbinaria turbinata*, in which the rhizoidal primitive leaves are profuse and the rest of the frond much reduced. Others are *Caulerpa verticillata*, species of *Ectocarpus*, Cyanophyceae and dendroid colonial diatoms. The epizoa include *Myrionema amboinense*, *Ostrea mordax*, and a large Zoonthid whose polyps (which expand only in the shade) have brown tentacles and a velvet-green disc. A group of these is shown in Plate XXI, fig. 4, half-contracted because of the sunshine. It is a curious fact that although the mangrove roots are in some places so extensively colonized by various organisms, elsewhere they are singularly clean and bare—a state which has been accepted as typical for *R. mucronata*.

The flora may be further characterized. The turf of *Thalassia*, though not universal, is widespread, even on areas which are awash or exposed at low water, and it attains, where thickest, a more luxuriant development than elsewhere on the reef. A notable feature is the abundance of *Halimeda Opuntia* in the turf; this is so marked that the sand in places is largely composed of dead fragments of this alga. *Caulerpa racemosa* and *Halophila ovalis* are other members of the turf, which has very considerable sand-binding properties, due mainly to the rhizomes of the *Thalassia*. A notable alga in the park is *Cystophyllum muricatum*, a species which attains a greater height above the substratum than any other form on the reef. *Caulerpa* may develop long creeping stolons, but *Cystophyllum* attains a height of 4–5 ft.; and with it occur species of *Sargassum*, including *S. lanceolatum*.

Of the animals listed on p. 44, the great majority may be found in the mangrove park; but some are more characteristic of it than others. Beyond the species mentioned, *Melarthaphe* may be found on the trees, and the large black *Pinna vexillum*, the mangrove hermit *Clibanarius striolatus*, and the blue and green crab *Thalamita crenata* are characteristic of the region. Forms which are special features of the park or have their headquarters there are the hydroid *Myrionema amboinense*, the enormous sprawling Holothurian *Synapta maculata* (Plate X, fig. 2), often 2 or 3 ft. long, and the black commercial sponge *Euspongia irregularis* var. *pertusa*. Other species which are very prevalent are the spider-shell *Pterocera crocata*, the round mud-coloured sponge *Cinachyra australiensis*, another sponge, *Spirastrella purpurea*, and the box-crab *Calappa hepatica*. *Holothuria argus*, though nowhere common, is confined to the park and the fringes of the swamp. Of all these animals, the one most distinctly characteristic of the park is *Myrionema amboinense*, a species with large brown polyps which grows on mangrove roots, on *Halimeda*, and on *Thalassia* leaves. This is prevalent where conditions are suitable over an area which includes the mangrove swamp and park, and extends somewhat towards the anchorage. Outside this region it is rarely found.

E. THE ROCKY AREA.

(Text-fig. 8.)

Mention has already been made of "honeycomb-rock." This is a descriptive term applied to a type of rock which occurs both on the reef flat and outside the rampart. Since the extent of this rock is important both from the point of view of the origin of the reef and from that of the arrangement of organisms, its distribution should be clearly appreciated, and is illustrated in Text-figs. 7 and 8. The rock in question occurs in the form

either of flattened slabs, often of considerable extent, or of more or less continuous pavement-like areas. The surface is irregular and the rock is honeycombed by pits and intricate crevices, and is attacked by boring organisms. The rock consists of dead coral, but probably in a modified form.*

Outside the rampart the honeycomb-rock is present along two stretches. The "windward shelf" of the key chart, a crescentic pavement fringing the windward arc of the reef, is composed of it; and the "south-west shelf" is a smaller area of similar nature. We do not wish to imply that honeycomb-rock inside and outside the rampart is of the same chemical composition and origin, though this may be the case. On the flat itself, inside the rampart, the rock occurs most extensively over a broad curved tract indicated by close stippling in Text-fig. 8. This tract starts at the rampart and runs at first northward and slightly westward, afterwards tending north-eastward in the direction of Tripneustes Spit; but becomes lost in the sandy part of the anchorage before the Spit is reached. This area is not wholly rocky, since it contains sandy pools and shingle-patches; nor is the rock equally developed all over it; but it is the region in which the rock is of maximal occurrence. As indicated in the figure by less close stippling, rocky areas occur also in the mangrove park east of the principal tract, and extend into some of the moat pools and on to the Thalamita flat. The contrast between these patches and the main tract is probably exaggerated in the figure; but the rock is on the whole more broken in the mangrove park than it is in the principal tract. It is this rocky tract, together with the rampart, which holds up the water in the south-eastern part of the mangrove park during the period of low water.

The rocky tract lies partly within the mangrove park, since part of it is colonized by trees or saplings of *Rhizophora*. The park, however, extends farther than the rocky tract, on to sandy ground, in the region between the anchorage and the mangrove swamp. The inhabitants of the rocky part of the park will resemble those of the rocky tract or those of the Thalamita flat according to the exact nature of the ground.

The fauna and flora of the rocky tract are not markedly distinct from that of any part of the reef flat where dead blocks of coral are present, but on it rock-haunting species are naturally somewhat concentrated. A striking feature in some places is the abundance of *Onchidium*. This soft and leathery pulmonate, similar in facies to a Dorid nudibranch, is seen by the score, out of water and exposed to the full power of the sun. On a single square yard fifteen individuals were counted. Other common inhabitants of the region are the mud-coloured, very hairy crab, *Pilumnus vespertilio*; the black or variegated brittle-star, *Ophiocoma scolopendrina*; *Cinachya australiensis*; *Acanthozostera gemmata*; and *Holothuria atra*, with its tail anchored beneath a block of coral or in a crevice. Attached lamellibranchs are naturally abundant (*Modiolus auriculatus*, *Spondylus ducalis*, *Chama jukesii*) and the rock is attacked by boring species. A low moss-like turf of algae often clothes the rock; this is variable in constitution from one place to another, but frequently includes *Laurencia*; *Boodlea* and *Dictyosphaeria* are also characteristic.

The shingle-banks F9 and F10 may conveniently be mentioned here. They are areas consisting of rampart material, and their fauna and flora resemble those of the rampart, grading imperceptibly, in the case of F9, into those of the Thalamita flat. A notable inhabitant of F9 is the calling-crab *Gelasimus tetragonon*.

* Sections and analyses will be published later.

F. THE THALAMITA FLAT.

This is a wide stretch of reef flat consisting in the main of sandy ground overlaid by slabs and boulders of dead coral, but also includes honeycomb rock. It is partly exposed at low water, partly under very shallow pools; but only exceptionally are the pools deep enough to contain a population resembling that of the moats. The sandy areas support *Thalassia* and *Halophila* as usual, and also *Spyridia filamentosa*. Except in the moat-like pools mentioned, and in the regions of transition from flat to moat, there is little living coral, such as exists being limited to shallow fringes of living *Porites* round the edges of dead slabs, and to small examples of *Favia*, *Cyphastrea*, etc.

The Thalamita flat is a region in which organisms characteristic of the undersides of movable slabs and boulders are particularly concentrated, though under similar boulders elsewhere a comparable range of life will be found. On the upper surfaces there are *Chama*, *Spondylus*, acorn-barnacles and limpets (*Siphonaria*), but the species of the undersides are more interesting. A striking feature here are the encrusting sponges, of which a number of species are common, and exhibit diverse and brilliant coloration. The list which follows will give some idea of the range both of species and colour. The algae of the region consist mainly of mossy growths in which *Laurencia*, *Boodlea* (and in the spring, *Hydroclathrus*) are dominant. *Dictyosphaeria* is widespread, and the underside forms include *Anadyomene*, nullipores and Squamariaceæ.

Another characteristic of the Thalamita flat is the abundance of *Hippopus hippopus* (Plate XVIII, fig. 1), adults of a similar range of size being evenly distributed. Young specimens are scarce.

LIST ILLUSTRATING THE FAUNA OF THE THALAMITA FLAT.

PORIFERA.

- Gellius fibulatus and the following encrusting forms:
 Chondrilla nucula.
 (Buff; greyish or pinkish lavender; liver-colour.)
 Chalina clathrata.
 (Black.)
 Chalina camerata.
 (Cream.)
 Desmacidon reptans.
 (Lilac-blue.)
 Ophlitaspongia rimosa.
 (Usually red or scarlet.)
 Rhaphidophylus coralliphilus.
 (Red.)
 Iotrochota purpurea.
 (Indigo-blue; dark blue; black.)
 Laxosuberites proteus.
 (Golden yellow.)
 Pseudosuberites andrewsi.
 (Brown.)

PORIFERA—continued.

- Polymastia sp.
 (Yellow.)
 Spirastrella semilunaris.
 (Probably includes scarlet, yellowish or reddish brown, and brilliant ultramarine forms.)
 Spirastrella aurivillii.
 (Flesh-colour.)

COELENTERATA.

- Phymanthus.
 Stoichactis kenti.
 Actinodendron plumosum.
 Dynamena crisioides.

POLYCHAETA.

- Iphone muricata.

BRACHYURA.

- Thalamita stimpsonii.
 Atergatis ocyroe.
 Pilumnus vespertilio.

GASTROPODA.

Trochus fenestratus.
Siphonaria denticulata.

LAMELLIBRANCHIA.

Spondylus ducalis.
Lima tenera.
Pinctada margaritifera.
Arca fusca.
Hippopus hippopus.
Chama jukesii.

ECHINODERMATA.

Ophiothrix longipeda.
Stichopus horrens.
Holothuria atra.
 „ *coluber*.
 „ *impatiens*.
 „ *leucospilota*.

ASCIDIACEA.

Didemnum candidum.
 „ *psammatotodes* var. *skeati*.

G. THE SANDY AREAS.

(Plate VIII, fig. 1.)

The Thalamita flat passes gradually along its northern side into the Sand flat. The latter is the most extensive sandy part of the reef flat, and has definite sandbanks (F2-4) between it and the anchorage. The region between anchorage and mangrove park, however, is also extensively sandy, and includes the sandbanks F6, 7 and 8. The region between F7 and 8 and the mangrove swamp, which lies partly within the limits of the mangrove park, is also so sandy that it may be considered with the others.

Some of the sandy areas are bare and free from plants, but usually there is at least a sparse growth of *Thalassia*, *Halophila*, or both; but whereas *Halophila* is sometimes dense, *Thalassia* is usually sparse, and often covered by epiphytes (*Spyridia filamentosa*, *Polysiphonia*, etc.). On the Sand flat, which is partly exposed at low water, partly covered by very shallow pools, *Thalassia* tends to keep to the pools, whereas *Halophila*, *Spyridia* and beard-like growths of Cyanophyceae occur freely both in pools and on the exposed parts. In April, 1929, these Cyanophyceae became notably abundant on various parts of the reef flat and in the anchorage, overgrowing and tending to smother living coral in the latter locality. On the Sand flat and Thalamita flat they were particularly prevalent on the eastern side. The form characteristic of the shallower areas is *Lyngbya majuscula*, but mixed with it is usually *Hormothamnium solutum*, which replaces it in the deeper pools. On Plate VIII, fig. 1, the desolate aspect of the Sand flat with its trailing beards of Cyanophyceae may be seen. A striking alga confined to sandy areas is *Avrainvillea erecta*, which was first noticed on 24th October 1928, and thereafter was abundant. The carrot-like stipes of this species, 6 or 8 in. long, is immersed in the sand, only the crown, which resembles a green sponge, projecting at the surface. *Caulerpa racemosa*, though present, plays no extensive part in sand-binding here. Both here and on the Thalamita flat *Sargassum* and *Cystophyllum* appear in pools.

The fauna of the sand is interesting and distinctive. The anemone *Actinodendron plumosum* is a characteristic form, burying its trumpet-shaped body in the sand and expanding its fern-like fronds (Plate XX, fig. 1) at the surface when covered by water. When exposed it partially contracts into its burrow, or lies with its upper parts collapsed at the surface. Most of the animals, however, live out of sight, either in burrows or buried in the sand. On p. 56 is a list of common or interesting species.

This list requires further comment. In the first place, it might be expected that among the worms some species of polychaet would be dominant. As far as we could ascertain by a good deal of digging this is not the case. The commonest "worm" is one

of the species of *Edwardsia*, which comes up in almost every spadeful of sand. After this, the very large *Balanoglossus carnosus* (the castings of which are visible on the surface, making an estimate of the population possible) is among the prevalent species; and other plentiful forms are geophyreae, such as *Aspidosiphon cumingii*, which resembles a piece of *Thalassia* root; the polychaet *Mesochaetopterus minuta* with its long thin tubes; and the attenuated *Phyllodoce malmgreni*. *Eurythoe complanata*, a handsome polychaet, is common on the reef, but occurs under boulders, etc., as well as in sand. Among the mollusca various forms are common. Naticidae of a number of species occur, more than those mentioned in the list. *Nassarius coronatus* is very common, and may be seen exploring the surface with a long feeler, either in pools or when the flat is covered by the tide. *Strombus gibberulus* is a leaping buried form; *S. luhuanus* sometimes occurs in large colonies, lying about the surface. *Terebra affinis* and *Clava vertagus* are the usual reward of anyone digging for the handsome pencil-shell *Terebra muscaria*. One of the most interesting forms is the giant squilla *Lysiosquilla maculata*, which makes a very deep burrow, some 3 in. in diameter, narrowed at the mouth by a circular shelf or diaphragm. *Ptychodera flava* (a small Enteropneust), and a sand-dwelling species of the Actinian genus *Phymanthus*, are locally abundant. The Cerianthid *Arachnanthus* was rarely seen.

If a complete list of the inhabitants of the sandy areas were to be made, it would contain not only typical sand-dwellers, such as those mentioned and many beside, but would also include a very considerable number of the species given in the list of typical reef-flat organisms on p. 44. This is due, however, simply to the fact that a certain number of scattered pieces of dead coral and specimens of *Hippopus* occur on predominantly sandy areas, and upon or beneath these the species in question are found.

SPECIES CHARACTERISTIC OF SANDY AREAS.

ANTHOZOA.

- Arachnanthus*.
- Edwardsia*, two species at least.
- Phymanthus*.
- Actinodendron plumosum*.

NEMERTINEA.

- Baseodiscus* (probably *B. quinquelineatus*).
- Species of *Lineus*.

POLYCHAETA.

- Eurythoe complanata*.
- Phyllodoce malmgreni*.
- Marphysa mossambica*.
- Scolecopsis indica*.
- Mesochaetopterus minuta*.

GEPHYREA.

- Aspidosiphon cumingii*.

CRUSTACEA DECAPODA.

- Callinassa australiensis*.
- Callinidea*.
- Macrophthalmus telescopicus*.

STOMATOPODA.

- Lysiosquilla maculata*.

GASTROPODA.

- Clava vertagus*.
- Natica gualteriana*.
- Uber flemingianum*.
- „ *mammilla*.
- Strombus gibberulus*.
- Nassarius coronatus*.
- Terebra affinis*.
- „ *muscaria*.

LAMELLIBRANCHIA.

- Loripes edentulus*.
- Corbis fimbriata*.
- Cardium oxygonum*.
- Tellina virgata*.
- Macra maculata*.

ECHINODERMATA.

- Archaster typicus*.
- Laganum depressum*.
- Holothuria arenicola*.

ENTEROPNEUSTA.

- Balanoglossus carnosus*.
- Ptychodera flava*.

THE RAMPARTS AND BOULDER TRACT.

A. THE OUTER RAMPART.

(Text-figs. 7 and 12; Plate XI; Plate XII, figs. 1 and 2; Plate XIII, fig. 1; Plate XXVII.)

The extent of the outer rampart may be appreciated at a glance from Text-fig. 12, where it is shown in solid black. With it have been included *Tripneustes* spit and *Asterina* spit, which, although they hardly belong to the rampart proper, may suitably be considered with it, since they resemble it both structurally and ecologically.

ENCROACHMENT OF THE RAMPART.—The inner edge of the rampart is abrupt, forming in most places a slight cliff or escarpment. Its neatness, and steep slope, suggest that it is being renewed by fresh additions of shingle, and is tending continually to encroach upon the flat or upon the inner rampart. That such encroachment does indeed take place is illustrated by four of our photographs. Plate XI, fig. 4, is a view from above, looking down upon a portion of the Madreporo moat. In the upper part of the figure living coral may be seen; in the lower part, shingle from the rampart which has fallen upon the coral. Plate XII, fig. 1, is a view including part of the outer rampart and part of the inner. The steep slope of the outer rampart is seen on the right, and at its foot a bush of *Avicennia officinalis*. The outer rampart just here encroached decidedly upon this bush during our year of residence. This figure also shows a secondary wave of clean shingle which is overrunning the main mass of the outer rampart. Such secondary waves are indicated on the key chart by dotted lines running across the bases of some of the inward promontories of the rampart (R3, R6, R7), and may be seen in the aerial photographs reproduced in Plate XXVII. Where this happens organisms characteristic of the inner rampart (isopods, ants, and *Avicennia*) tend to appear on the piece of outer rampart cut off by the new shingle wave. Plate XIII, fig. 1, illustrates a case in which long spits of outer-rampart shingle have overrun the inner rampart.

Where the escarpments of either the outer or the inner ramparts descend to a moat or pool, the interstices of the shingle may harbour an interesting fauna. In the case of the pond P9 and neighbouring regions, for instance, there is a large population of the small actinian *Anemonia citrina*, as many as 40 specimens being found on one fragment of shingle.

THE RAMPART AS A HABITAT.—The outer rampart offers at first sight a most unpromising field for colonization by plants or animals. It resembles an ordinary pebble-beach, but, instead of pebbles, consists of loose fragments of dead coral and shells (Plate XI, fig. 3). This debris includes the remains of a variety of corals, but species belonging to the genus *Acropora* predominate. Although as a habitat the rampart is, therefore, in a certain degree unstable, its stability (except, presumably, in abnormally heavy weather) is greater than appears, since the angular and nodulated nature of the shingle fragments results in a good deal of interlocking, in addition to which they function as breakwaters. There is very little tendency towards any cementing of the fragments, at least near the surface; and although nullipores in the form of thin crusts are a feature of the rampart, they have here no binding power and make no continuous sheets of growth such as characterize the Outer Barrier. In spite, however, of the limitations of the rampart as an environment for life, it conceals an enormously populous fauna, particularly of small crabs and gastropods, under the fragments. Very little surface life is visible.

VARIATION IN LEVEL AND CORRELATED ZONATION.—The key to the distribution of life on the rampart is provided by a map, for which we are indebted to M. D. Glynne, and which illustrates the distribution of the encrusting nullipores upon it. These are arranged in a series of band-like zones running parallel to the general course of the rampart. The map will be reproduced and fully described in Tandy's systematic report on the algæ; but the essential point which it illustrates is that the zonation of nullipores conforms to the following plan:

1. In the highest and driest parts nullipores are absent or nearly so.
2. In a zone slightly nearer the sea they are slightly developed *under* fragments.
3. In the next zone to seaward they are moderately developed and visible *on the surface*.
4. In the last zone nullipores are *plentiful* on the surface, so that the ground is visibly purplish with them.

The zonation of other forms of life follows this plan, and it depends principally upon level. The rampart reaches higher levels along the stretch between the mangroves and the sea than it does to westward. From near the point M6 it slopes gradually downward in a westerly direction to the gap B, becoming slightly higher again on the stretch RA, but nowhere as high as to eastward. This means that in its western part the highest zone, in which nullipores do not exist, is absent. Other effects of level are due to the facts that the highest parts are the longest exposed during the period of low water; and that in many places the lower parts are kept moist during the ebb by water trickling off the flat, which, it will be remembered, is on a higher level than the sea outside the rampart at low water of a spring tide. Regions in which this trickling is well marked are indicated on the key chart as "trickle-zone." In certain places in this zone there is, contrary to the general rule, a binding of the shingle by turfs of algae (Plate XIX, figs. 2 and 4), the most remarkable of which is a form of *Caulerpa racemosa*. Some idea of the zonation of the rampart may be formed from Plate XXVII.

In the highest and driest parts of the rampart little life is to be found beyond rapidly moving isopods. With the exception of these regions, the rampart shelters a number of creatures, mostly under the shingle, some of which are very abundant—small gastropods (especially species of *Nerita*) and crabs (including many rapid scuttlers) predominate, but there are also echinoderms (*Asterina exigua*, *Echinometra mathaei*, and small holothurians), small hermits, lamellibranchs and anemones. Some of these forms, especially the mollusca, probably exhibit fairly precise zonation according to level, but we were unable to make any detailed study of it.

GAPS IN THE RAMPART.—The gaps which occur in the rampart, and which are marked A, B, C and D on the key chart, are not actual interruptions in its course, but merely low places through which the tide flows before the rampart in general is submerged. Their fauna and flora is slightly modified as a result of these conditions.

THE BOULDER ZONE OF THE RAMPART.—Along its seaward margin the rampart merges either into the windward shelf or into a zone in which boulders are conspicuous ("boulder zone" of the key chart). Here the fauna and flora become more varied, but it is impossible to draw any hard and fast line ecologically between the seaward edge of the rampart and the shoreward parts of these other regions. The boulder zone has a rather characteristic population, the nature of which may be judged from the following list, in which a number of its common animals are marked with asterisks. The algae are

enumerated farther on, on p. 68. The population of individual boulders depends, of course, partly upon the level at which they occur.

ORGANISMS CHARACTERISTIC OF THE OUTER RAMPART AND BOULDER TRACT.—The following list covers the boulder *tract* as well as the rampart and its boulder *zone*. The species cannot be listed separately for these areas, since the series characteristic of each run into one another, and sufficient indication has already been given of the manner in which the various forms are arranged. The list illustrates the predominance of mollusca and crustacea over other groups of animals; it includes a number of forms capable of withstanding arid conditions of one sort or another during the period of low water; and forms which can make the best of the unpromising environment presented by a shingle bank. Shells of the cat's-eye (*Turbo petholatus*) are common on the rampart, but we have not taken the living animal, even when diving.

ANIMALS CHARACTERISTIC OF OUTER RAMPART AND BOULDER TRACT.

(A number of species common in the boulder zone of the rampart are marked with asterisks.)

COELENTERATA.

Small anemones of the *Anthopleura* and

Phellia types.

Dynamena crisioides.

SIPUNCULOIDEA.

**Aspidosiphon*.

**Cloeosiphon*.

**Physcosoma*.

CIRRIPEdia.

Acorn-barnacles.

ISOPODA.

Ligia australiensis.

AMPHIPODA.

Locally abundant; including a species of *Hyale*.

ANOMURA.

Clibanarius virescens.

Petrolisthes lamarcki.

BRACHYURA.

Thalamita admete.

Chlorodopsis melanochirus.

Actaea tomentosa.

Atergatis ocyroe.

Phymodius unguatus.

Leptodius exaratus.

„ *nudipes*.

Metopograpsus messor.

STOMATOPODA.

Gonodactylus chiragra.

AMPHINEURA.

**Acanthozostera gemmata*.

Schizochiton incisus.

GASTROPODA.

**Trochus niloticus*.

Turbo nivosus.

„ *porphyrites*.

Nerita albicilla.

GASTROPODA—continued.

Nerita chamaeleon.

„ *plicata*.

„ *polita*.

„ *striata*.

Planaxis sulcatus.

**Cypraea annulus*.

„ *errones*.

Drupa marginalba.

„ *tuberculata*.

**Siphonaria denticulata*.

**Onchidium*.

LAMELLIBRANCHIA.

**Ostrea mordax*.

Melina nucleus.

Modiolus auriculatus.

**Lithophaga argentea*.

* „ *cumingiana*.

* „ *obesa*.

* „ *subula*.

* „ *teres*.

Arca fusca.

* „ *imbricata*.

**Tridacna crocea*.

**Gastrochaena gigantea*.

ECHINODERMATA.

Asterina exigua.

Echinometra mathaei.

Ophiocoma scolopendrina.

Small or young *Holothurians*, including

Polycheira rufescens.

Holothuria erinaceus.

„ *leucospilota*.

„ *pardalis*.

ASCIDIACEA.

**Didemnum candidum*.

B. THE BOULDER TRACT.

(Plate V, figs. 3 and 4.)

This region calls for little in the way of special comment. It is the tract along which the boulders of dead coral attain a larger average size than elsewhere, and it contains also a proportion of smaller coral fragments and some shingle. Its flora and fauna are, therefore, a reflection of those of the rampart and boulder zone already described. A feature of special interest is the notable boulder covered with *Ostrea mordax* and illustrated in Plate V, fig. 4, which has already been described (p. 36). The tract is a region particularly favourable for the study of the boring lamellibranchs and gephyreans which are a general feature of coral rock and boulders on the reef. These are described fully in a report by G. W. Otter elsewhere in this series, but it may be mentioned here that they include several species of the genera *Lithophaga* and *Gastrochaena*, as well as other forms, such as *Modiolus cinnamomeus*, *Petricola lapicida*, etc. *Tridacna crocea* is one of the most notable borers, since it is present in incredible numbers and is responsible for the excavation of cavities of considerable size. This species is illustrated in Plate VI, figs. 3 and 4, in different degrees of submergence in the surrounding coral. It is often buried so fully that the expanded mantle is flush with the surface. The gephyreans include a number of Sipunculid forms belonging to the genera *Aspidosiphon*, *Cloeosiphon*, *Physcosoma*, etc., notable among them being a species of *Aspidosiphon*, a stout worm with a conical striated extremity more than a centimetre in diameter.

Some of these animals are of relatively large size, and make very considerable burrows in the coral; the total population of them is enormous, and considered as a unit in reef economy they represent a very powerful destructive agency.

C. THE INNER RAMPART.

(Text-figs. 7 and 15; Plate XII, figs. 1, 3 and 4; Plate XIII, figs. 1-3; Plate XXVII.)

This region differs from the outer rampart rather sharply in an ecological sense.

In the first place the area is extensively colonized by certain flowering plants, which show some relation to tide levels. Immediately inside the outer rampart young seedlings and saplings of *Rhizophora mucronata* may be seen (Plate XI, fig. 2), and near the edge of the mangrove swamp are a number of outlying specimens of it, in a dead or dying condition (Plate XIII, fig. 3). Bushes of *Avicennia officinalis* (Plate XII, fig. 3), often distorted in shape, are scattered over the inner rampart, and another interesting plant is *Aegialitis annulata*. On the higher parts the shingle is extensively covered by the creeping *Sesuvium Portulacastrum* (Plate XIX, fig. 3). Indeed, at the end of the shingle tongue R2 there is a field of it some 100 yds. long by 30 wide (Plate XII, fig. 4, and Plate XXVII). The isolated patches of inner rampart at either end of the main area (IR1, 2, 3 and 17) have a fairly dense population of *Avicennia*, together with vestigial representatives of *Rhizophora* and some *Aegialitis*. It is a curious fact that on this reef the main population of *Avicennia* lies between the mangrove swamp (*i. e.* the home of the main population of *Rhizophora*) and the sea. This, in a coastal area of even slope, would be the other way round; but at Low Isles the inner rampart is *higher* in level than the floor of the *Rhizophora*-swamp, hence the inversion.

The fauna of the inner rampart exhibits a mingling of outer rampart species with forms characteristic of the shingle tongues inside the mangrove area, and includes the species listed below. Small gastropods and crabs are the dominant forms. The fauna of the moat-like pools which occupy the angle between the inner and outer ramparts has already been described; and it is only necessary to add that in regions bordering on such pools, and in other places where the surface is damper than usual, the fauna becomes somewhat modified, and richer in species. With regard to the calling-crab of the inner rampart, *Gelasimus tetragonon*, which sometimes makes its burrows in extraordinarily hard material, this species is known to occur at Low Isles only in areas outside the mangrove swamp. It inhabits the shingle-bank F9 as well as several parts of the inner rampart.

SPECIES CHARACTERISTIC OF INNER RAMPART.

ISOPODA.

Ligia australiensis.

ANOMURA.

Clibanarius virescens.

Petrolisthes lamarecki.

BRACHYURA.

Scylla serrata.

Leptodius exaratus.

Sesarma bidens.

„ *villosa*.

Metopograpsus messor.

Gelasimus tetragonon.

INSECTA.

Ants.

AMPHINEURA.

Acanthozostera gemmata.

GASTROPODA.

Turbo porphyrites.

Nerita albicilla.

„ *plicata*.

„ *striata*.

Bembicium melanostoma.

Tectarius malaccanus.

Melarthaphe scabra.

„ *undulata*.

Planaxis sulcatus.

Quoyia decollata.

THE ANCHORAGE.*

(Plate V, fig. 1; Plate XIV.)

In describing the reef flat enough has been said to cover the shallower regions bordering the anchorage. It remains therefore only to consider the reefs of dead coral rock, overgrown by living coral, which fringe it. These are labelled A1-5 on the key chart.

In the anchorage and the other seaward slopes of the reef, we are dealing for the first time with zones in which a varied growth of living coral and alcyonaria in a flourishing condition is the primary characteristic. In the moats, it is true, coral growth of a peculiar description is abundant, but it is restricted to a small number of species; and although in a pool such as the western moat a considerable number of coral species are represented, they cannot, apart from the special moat species, be described as constituting a flourishing growth. In the anchorage and on the seaward slope, however, wherever there is sufficient depth of water, and so long as no special local conditions of a limiting nature prevail, corals abound both in species and individuals, and form rich and varied fields of growth. Some idea of the extent and variety of such living coral may be gained from Plate XV,

* The anchorage, although its floor forms part of the general seaward slope of the reef, is an inlet in which special conditions prevail, and is therefore treated separately here.

which shows, in a diagrammatic form, the corals in an area some 6 ft. wide and 8 ft. long in the anchorage. It will be observed that almost the whole field here is occupied by living and overlapping colonies, so that the area of bare rock exposed is very slight.

The reefs of the anchorage consist of very irregular masses of dead coral, with sand, or sand and debris, between them. As the floor of the anchorage slopes downwards away from the shore, the height of such of these masses as reach the level of low water naturally increases. Near the shore, therefore, the pools or channels between them are shallow, becoming deep further out. The seaward margins of the reefs are usually somewhat abrupt.

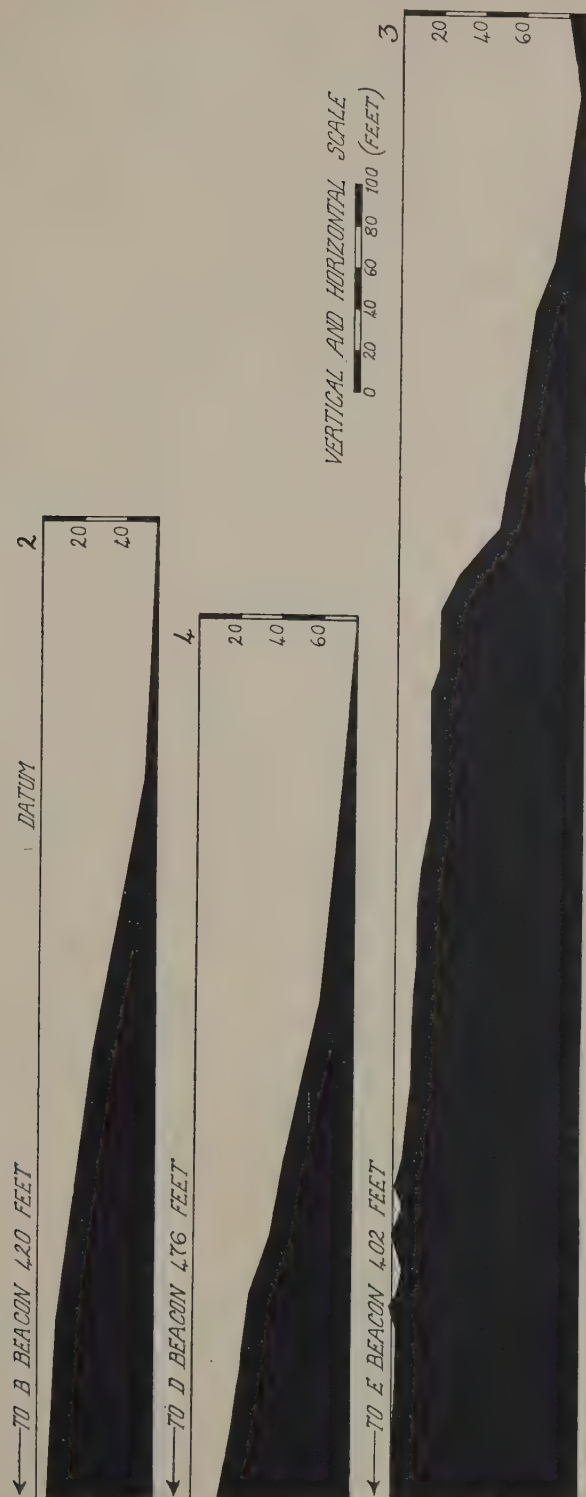
The greater part of the area of these reefs is accessible only at low spring tides. The degree of their exposure may be illustrated by an example. Luana reef, across which a level traverse was taken, is divided rather distinctly into a slightly higher landward part (A1) and a lower seaward portion (A2). The landward region uncovers at any tide which falls to a level 0.8 ft. above datum. The seaward part is submerged at such a tide, but at the lowest springs (the extreme recorded being 0.4 ft. below datum) its highest parts are exposed; its deeper regions are therefore always submerged.

AREAS OF HIGH LEVEL.—The region A1 just mentioned is of particular interest. As a result of its level it is exposed or awash more frequently and for longer periods than the rest of Luana reef, though submerged at neaps. This difference, though slight, is enough to modify its coral fauna distinctly. A considerable part of the area is occupied by a platform-like growth of *Montipora ramosa*, with *Acropora hebes* and other corals, somewhat similar to the growth in the moats. Beside these are various other corals and alcyonaria, numerous clams, holothurians and other animals, and a considerable growth of certain algae. The most interesting feature, however, is the presence of a quantity of a species of *Acropora* with slender buff-coloured branches and pale blue tips. This species (*A. pulchra*) makes large rounded bushes or tufts (Plate IX, fig. 2), or even platforms, which are exposed at low spring tides, and which occur chiefly on the more seaward part of the area. This coral appears to be characteristic of a somewhat precisely limited zone of the shore, occurring normally neither above nor below the region peculiar to it. It may be found, however, in any suitable position on the Low Isles reef which is directly open to deep water and which lies at the level required (just above datum).

On other anchorage reefs there occur certain areas of similar level to A1—for instance, the middle of the island-like reef A3—but they are less interesting. In Plate XIV, fig. 1, a view from the top of the lighthouse shows most of the area A1 and also the higher parts of A3, with a deep channel between. This photograph was taken at a state of the tide which left A1 exposed and the more seaward part of the same reef (A2) still under water. This brings out well the difference in level between A1 and A2, the latter area being dimly visible beneath the water.

AREAS OF LOWER LEVEL.—On the seaward part of Luana reef and in comparable regions the coral growth at once becomes denser and more varied, although naturally richer in some places than in others. Plate XV represents a portion of A2 close to the channel which separates it from A3. Plate XIV, fig. 2, illustrates the growth at a point nearer the shore.

The coral fauna of these reefs is characterized by the abundance of species belonging to the genus *Acropora*, but presenting widely varied aspects. Some of them form large salver-shaped or bracket-like structures with a stout central or eccentric stalk or region of attachment; others form bushes or straggling areas of stag's-horn-like branches; still



TEXT-FIG. 9.—Sections of the seaward slopes of the Low Isles Reef. Their positions on the reef are indicated in Text-fig. 11, each section bearing the same number here as in Text-fig. 11. The slopes are described on p. 64.

others make finely divided bushy growths of completely different facies. Another dominant series are the foliose species of *Montipora* also illustrated in Plate XV. Beyond these a variety of other forms are represented. We do not propose to describe the growth-forms and ecological relationships of the coral fauna here, because, in considering the ecology of the reef as a whole, we feel that our account will be the more intelligible if digressions dealing with corals in particular are avoided. Discussions of the ecology of corals will be found, however, in papers farther on in this volume.

The alcyonaria, no less than the corals, find their proper habitat in the anchorage and on the seaward slope. They are not wholly absent from the flat, but are of occasional occurrence there, and do not attain a large size; they possess no representatives which flourish actively under moat conditions. In the regions to which open water has access at all states of the tide, they become represented in hardly lesser degree than the corals, exhibiting great abundance of species and occupying a large amount of space as individuals. Specimens of *Sarcophytum* from 2-4 ft. across are not rare (Plate XVI, fig. 1), and fields of *Simularia* covering yards of rock also occur (Plate XVI, fig. 2). Specimens of some of the large fleshy species may occur at levels where they are liable to exposure at low water (Plate XVI, fig. 3). These lie flaccid until the water returns, when they become turgid once more and appear to be none the worse.

FAUNA AND FLORA OF THE ANCHORAGE.—The nature of the fauna and flora of the anchorage may be gathered from the list on p. 67. This list includes the rest of the seaward slope as well as the anchorage, but the majority of the forms mentioned are common to both. In the anchorage the variety of animals other than corals and alcyonaria is considerable, despite the prevalence of forms belonging to these groups. Clams in particular are abundant, and algae are well represented on the higher levels. As levels below low water of springs are reached, however, algal growth becomes very poor, and corals, clams and alcyonaria appear to be completely dominant. In April 1929, the coral became much infested by a beard-like alga similar to *Lyngbya majuscula*.

THE SEAWARD SLOPES OF THE REEF.

(Text-figs. 9-11; Plate XVII, fig. 1.)

THE CONFIGURATION OF THE SLOPES.—From the outer rampart and the boulder tract, the reef descends to the muddy floor which surrounds it. The slopes are everywhere rocky except in the anchorage. We owe our knowledge of the configuration of these slopes to soundings taken by M. A. Spender, with the assistance of Anne Stephenson. Some of the lines of soundings have been tabulated in the form of sections, and are reproduced in Text-fig. 9. The positions of these several sections on the reef are indicated in Text-fig. 11 (p. 68).

It will be evident from section 3 in Text-fig. 9 that at the windward arc of the reef the seaward slope is at first gradual; but when a depth of 21 ft. (6·4 metres) is reached, it suddenly becomes steep, descending to 48 ft. (14·6 m.) in the next 13 yards. The slope here, therefore, reaches the inclination of 1 ft. in 1·4. From the bottom of this descent the slope becomes more gradual again, until it reaches 86 ft. (26·2 m.) at a distance of 360 yards from E beacon. From that depth to seaward the level rises again slightly, to 70·5 ft. (21·5 m.); in other words, there is a slight trough at the foot of the slope.

Neither of the sections 2 and 4 reveals anything as remarkable as this; but both indicate the same tendency towards a gradual slope from the shore-line, followed first by a steeper slope and then by a more gradual one. The steeper part begins at comparable distances (about 170–190 yards) from the shore* but the slope varies from 1 in 4·2 to 1 in 6·2, and does not approach the inclination which occurs at the windward arc. The maximum depths reached along these sections vary from 55 ft. (16·8 m.) to 76 ft. (23·2 m.) at distances of some 300 yards from the shore. The steeper of the two slopes and the one descending to the greatest depth (apart, of course, from the windward slope first described) lies off the extreme western corner of the reef (section 4).

Other lines of soundings not illustrated here provide further data. The most important of them was taken to leeward of the boulder tract (5, in Text-fig. 11). Here the slope is in the main quite gradual, the maximum depth reached being 37 ft. (11·3 m.) at 294 yards from the boulder tract. There is, in fact, a shoal to leeward of the reef, which deepens gradually and merges into the 11- to 12-fathom level some three miles to the north-west. Numerous soundings off the mouth of the anchorage give depths of 21 to 29 ft. (6·4 to 8·8 m.).

THE FAUNA AND FLORA OF THE SLOPES.

THE FRINGE TO SEAWARD OF THE RAMPART.—The zone of boulders into which the rampart merges along much of its extent has already been mentioned (p. 58), but a further note is required regarding the “windward shelf” and “south-west shelf” of the key chart.

The windward shelf is a pavement of pitted honeycomb-rock, considerably overgrown by a felt of algae. There are boulders and debris on its surface. The algal flora of the honeycomb-rock and boulder zone includes the forms listed on p. 68, but among these the brown alga *Sargassum cristaefolium* is particularly noteworthy. This species is a form of higher growth than most of the others, and is more or less abundant all along the windward shelf, where it constitutes a distinct “*Sargassum* zone,” in which *Turbinaria ornata* is also a characteristic element. The algal zone in general is widest and most luxuriant at the weather extremity of the reef, and the growth of *Sargassum* at its best where the trickle from the rampart is well marked. The strip of *S. cristaefolium* and *T. ornata* is also represented outside the stretch of rampart RA. The well-known *Chlorodesmis comosa*, forming tufts of the most brilliant green, is found both on the windward shelf and on the south-west shelf. It is a form characteristic of the Outer Barrier and of the outer slopes of Batt Reef, but does not occur on the flat at Low Isles. An interesting animal to be found both in the boulder zone and off shore is a species of the Zoanthid genus *Palythoa*, large masses of which may be completely exposed at low water (Plate VI, fig. 3.).

THE PRINCIPAL SLOPE (Text-figs. 9 and 10; Plate XVII, fig. 1).—From the windward shelf or the boulder zone the transition to the region of effective coral growth is usually gradual, though more rapid in some places than in others. At first small, low or isolated colonies of corals and alcyonaria appear, but as the water deepens these rapidly increase in size and number until a rich growth is attained. The seaward slope, however, is not covered uniformly by a carpet of coral. The surface of the slope, to begin with, is not smooth, nor merely slightly irregular; it is in most places definitely rugged, being covered by fixed blocks of dead coral of varying shape. These blocks are low and broad near the

* *I. e.* from B and D beacons respectively.

shore, but as the depth of the water increases, they tend to become higher, and many of them form very large mounds. From the shore outwards for some distance, the tops of a number of these mounds are at such a level that they are exposed at low water of exceptional tides. These masses may be as much as 20 by 25 ft. across the top, with sides 20 ft. or more deep, which are frequently precipitous or overhanging, so much so that in the extreme cases the mass becomes more or less mushroom-shaped. It is the tendency of coral to grow on top of these masses of rock, and down their sides. Overhanging surfaces present a sparser growth, and many of the species characteristic of them are forms which rarely if ever appear in the more sunlit positions. The floor of the slopes between the rocky masses is usually either bare or but poorly colonized.

Much of what has just been described lies beyond the level of low water of the most extreme tide, between that and a depth of some 5 fathoms. The description of this submerged region is based upon examinations of the slope made with the assistance of a diving helmet, supplemented by a study with a water telescope used from a boat.

The belt of rich coral growth encircles the whole reef. At the same time it is more luxuriantly developed in some places than in others, and differences exist in the range



TEXT-FIG. 10.—Section of a slope to leeward of Low Isles, illustrating the arrangement of coral masses upon it. For comparison with Plate. XVII, fig. 1; see also p. 65. This section is not based upon data as precise as those reproduced in Text-fig. 9, but is founded upon information sufficiently definite to give it an approximate accuracy. The vertical and horizontal scales are the same.

of species and growth-forms represented, as well as in other respects, between the windward and leeward sides. The “coral heads”* or mounds of rock overgrown by living coral, reach their most exaggerated form on the leeward side. A distinct zonation of coral species on the slopes is recognizable. The subject of this paragraph will be considered more fully in subsequent papers.

Before closing our account of the seaward slope and anchorage, we must mention an important but elusive section of the fauna. Wherever and whenever one dives in these regions, the water is seen to be populated by innumerable fishes. The brilliant and varied species characteristic of coral reefs abound, and the total population must be enormous. Many of the smaller fish are commensal with coral, as many as forty or fifty sheltering among the branches of a single colony of moderate size. We have seen some of these fish eating living alcyonaria, and others nibbling microphytic algae from the rock. We have not seen living coral attacked, but if part of a colony dies that portion may be devoured at once.

* We have not used the terms “niggerhead” or “negrohead” in this report, because they seem to involve ambiguity. We refer to stranded blocks of dead coral as “boulders,” and to masses of dead coral covered by a living growth as “coral heads,” this latter being the usage of the pilot-books.

Other interesting inhabitants of the slopes are mentioned in the following list. Noteworthy among them are the handsome stinging hydroid *Lytocarpus phoeniceus*, the urchin *Echinostrephus molare*, which makes deep burrows in solid rock, and the commercial *Trochus* (*T. niloticus*), which reaches its maximum in the seaward part of the boulder zone and thence downward.

ANIMALS CHARACTERISTIC OF SEAWARD SLOPES AND ANCHORAGE.

(Most, if not all, the genera of corals and alcyonaria here mentioned are common to both seaward slopes and anchorage; but certain species of some of the genera are characteristic of the windward side and others of the leeward. Certain species belonging to the genera marked with an asterisk are characteristic of vertical or overhanging surfaces below the level of low water.)

HYDROZOA.

Lytocarpus phoeniceus.
Millepora.

ALCYONARIA.

Clavularia.
Pachyclavularia.
Xenia.
Heteroxenia.
Cespitularia.
Alcyonium.
Sarcophytum.
Lobophytum.
Sinularia.
Heliopora.
Lithophytum.
**Dendronephthya*.
**Juncella*.
**Melitodes*.

ANTIPATHARIA.

**Eucirripathes*.

ZOANTHINARIA.

Palythoa.

MADREPORARIA.

Seriatopora.
Pocillopora.
Stylophora.
Euphyllia.
Orbicella.
Cyphastrea.
Leptastrea.
**Echinopora*.
Galaxea.
Favia.
Platygyra.
Coeloria.
Hydnophora.

MADREPORARIA—continued.

Symphyllia.
Lobophyllia.
Oulophyllia.
Tridacophyllia.
**Merulina*.
Fungia.
Herpetolitha.
Polyphyllia.
Pachyseris.
Pavona.
Psammocora.
Diploastrea.
**Dendrophyllia*.
Astreopora.
**Turbinaria*.
**Montipora*.
Acropora.
Goniopora.
**Porites*.

POLYCHAETA.

Spirobranchus giganteus.

CRUSTACEA.

Panulirus versicolor.

MOLLUSCA.

Trochus niloticus.
Pinctada margaritifera.
Tridacna crocea.
„ *derasa*.
„ *fossor*.

ECHINODERMATA.

Linckia laevigata.
Echinostrephus molare.
Stichopus chloronotus.
Lamprometra gyges and other crinoids.

ALGAE OF THE WINDWARD SHELF AND BOULDER ZONE.

(The great majority of these species occur also in the anchorage, though some are more plentiful there than others. The three species marked with an asterisk are particularly characteristic of the windward side of the reef.)

PHAEOPHYCEAE.

**Sargassum cristaeifolium*.

**Turbinaria ornata*.

Dictyota Bartayresiana.

„ *ciliata*.

Padina australis.

„ *Commersoni*.

CHLOROPHYCEAE.

Caulerpa racemosa.

Halimeda cuneata.

„ *Opuntia*.

Tuna.

**Chlorodesmis comosa*.

Bornetella nitida.

CHLOROPHYCEAE—continued.

Dictyosphaeria favulosa.

„ *sericea*.

„ *Versluysii*.

Boodlea paradoxa.

FLORIDEAE.

Galaxaura spp.

Laurencia botryoides.

„ *papillosa*.

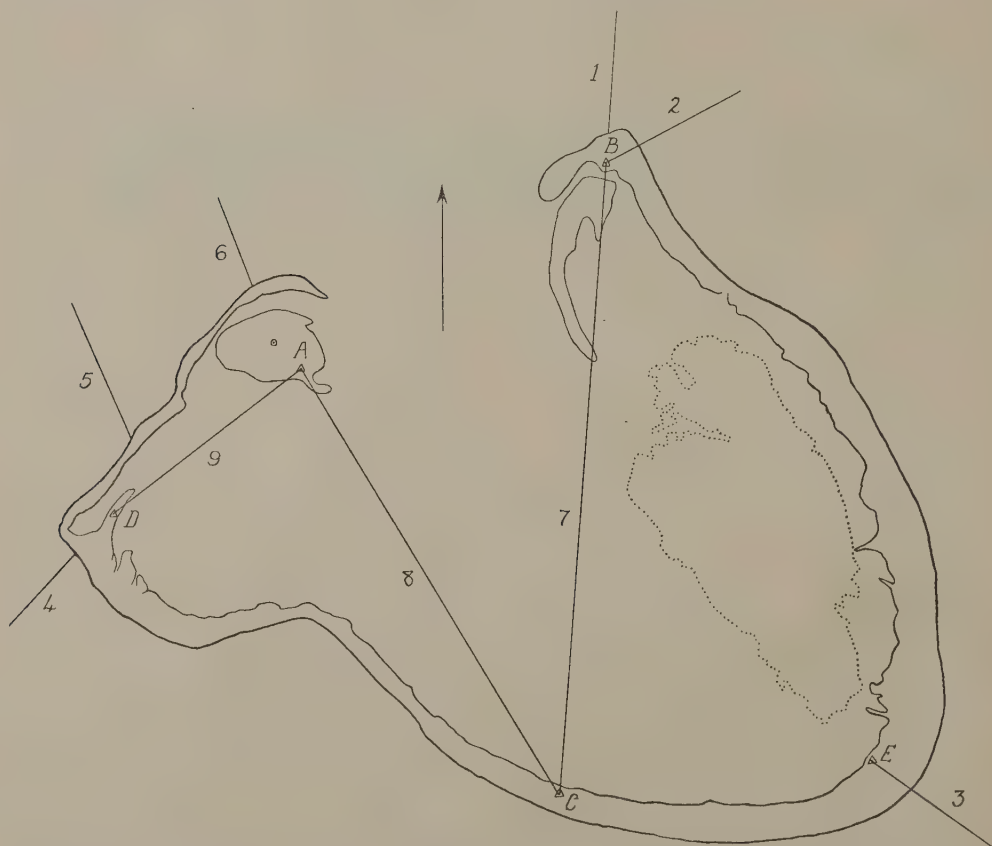
Digenea simplex.

Amphiroa fragilissima.

Melobesia.

CYANOPHYCEAE.

Well represented.



TEXT-FIG. 11.—To show the approximate positions on the Low Isles reef of the several sections reproduced in Text-figs. 7 and 9, and of certain other sections. The letters A-E indicate the positions of beacons. Sections bear the same numbers in figs. 7, 9 and 11.

REVIEW OF THE LOW ISLES FAUNA AND FLORA.

(By T. A. STEPHENSON.)

There are a number of points relating to groups of animals in general, which could not be brought out in the preceding regional treatment of Low Isles. So far the regions have been classified, and the animals treated as they came; if we now consider the animal groups one by one, some further relevant points will become evident. Such generalizations relating to algae as have not yet been stressed will be dealt with by Tandy in his systematic report on that group. In the case of the animals, since there will be no general report, but a large number of separate ones, it is advisable to make a short general statement here. Before leaving the plants altogether, however, I should like to enumerate a few features which are bound to strike any naturalist familiar with the intertidal regions of temperate seas, on comparing them with a coral reef.

On a typical rocky shore in a temperate region, whether it be Cornwall or Sydney, one of the most apparent features is the abundance and variety of the larger algae. Some of these inhabit high levels, some live in rock-pools, and others constitute the familiar "Laminarian zone" uncovered at spring tides, in which a dense growth of large algae of the family Laminariaceae (or in the Sydney area of their Australian counterparts, *Ecklonia*, *Sargassum*, *Cystophora*) is the dominant feature, the plants often reaching a length of several feet. On a coral reef such as Low Isles there is an immediate contrast. There is no Fucoid growth at high levels (though *Enteromorpha* may occur as on a temperate shore); the pools contain, it is true, an abundance of algae; but these are mostly not of the showy type characteristic of cooler seas, but are mossy or turf-like forms; and far from there being any Laminarian zone or comparable region, the lower levels of the shore are those in which corals are dominant and algal growth weak. The only large algae at Low Isles are brown species belonging to the genera *Sargassum*, *Cystophyllum*, *Turbinaria* and *Padina*. These make a fair growth in pools on the flat; and there is the *Sargassum*-zone already described on the windward shelf; but these features are but pale reflections of the growth in a well-stocked temperate rockpool, or in a Laminarian zone.

Another feature of coral reefs is the widespread occurrence of the nullipores (Melobesieae). These are fairly plentiful on temperate shores, but at Low Isles are almost ubiquitous in the form of thin crusts or small nodular growths, whilst on the Outer Barrier the superficial covering of Melobesieae in certain zones of the reef is so continuous and universal that much of the substratum is made pink by it. On still other reefs, of types not within our experience, the Melobesieae become massive, and may be classed among the important contributors to the bulk of the reef. At Low Isles they play a limited part in reef-formation.

Again, Low Isles is distinguished by its very extensive flora of Cyanophyceae. The abundance and variety of these dingy organisms is one of the striking features of the reef. They occur in the form of rust- or beard-like growths, as scabs on the sand, and under other manifestations, in every available type of habitat except the very driest places.

Two other sections of the algal flora are of special interest. Firstly, the vast quantities of unicellular algae or Zooxanthellae, which abound in the tissues of nearly all the reef corals as well as in those of clams, hydroids, and other animals, are responsible in great measure for the supersaturation of the water with oxygen, which occurs during certain phases of the diurnal cycle, in shallow pools containing abundant coral. This supersaturation, though relatively slight in regions such as the anchorage which are always in direct connection with the sea, is perceptible wherever coral growth is dense. It is difficult to judge the effect which this may have on the organisms exposed to it; especially as it is offset by the fact that wherever supersaturation becomes highest during the day, there will the oxygen content of the water be lowest during the night; and indeed on the flat it falls so low at night as to approach the lethal limit for fish, though not for coral. A second group of algae, interesting from a chemical point of view, are certain of the Valoniaceae (*Dictyosphaeria*, *Valonia*, etc.). Species of *Valonia* and *Halicystis* have been studied by S. C. and M. M. Brooks (1929, 1930), who have shown that the cells of these forms exercise selective accumulation of potassium, and resist the entry of sodium. The pH of the intracellular sap of *Valonia macrophysa* under normal conditions is about 6.2, the potassium and sodium ion concentration being roughly 0.5 M. and 0.1 M. The corresponding values for sea-water are pH 8.2; potassium 0.01 M.; sodium 0.5 M.

Turning to the animals, certain general features at once appear. In the proper regions the corals and alcyonaria dominate; but apart from these the mollusca form the most extensive element in the fauna. T. Iredale collected mollusca of several hundred species at Low Isles, and a similar number at Three Isles. After these come the crustacea, with a varied and abundant series, of crabs and prawns in particular. The echinoderms, sponges and fishes are also well represented.

Another interesting point is the contrast exhibited by the rocky regions of higher level as between Low Isles and a temperate shore. On many British shores acorn-barnacles or mussels are dominant at certain levels, forming sheets so extensive as to crowd out other forms of life, apart from such species as can utilize the interstices between them. In the Sydney region, instead of these sheets of barnacles one finds an equally dense growth of the calcareous tubes of the worm *Galeolaria caespitosa*. At Low Isles, on the contrary, although acorn-barnacles are common, they never occur in anything approaching their abundance in temperate waters; and the organism which replaces them is *Ostrea mordax*, which may cover a rock so densely as to conceal it completely.

The groups of animals may now be reviewed serially, so that the relative abundance of their members, together with other points, may be indicated.

PROTOZOA.

An important feature here is the abundance of the large macroscopic foraminiferan *Orbitolites complanata* (Plate XIX, fig. 1). This, though more abundant in one place than another, is widespread over the reef flat. Its shells form an important element in the coarser grades of sediment on the reef, since Foraminiferan material (which must include a high proportion of *Orbitolites*) is estimated by Marshall and Orr as constituting somewhere near 20% of the sand. They also state that living flagellates, ciliates and diatoms are present among the fine detritus found in the sediment.* It should be noted further that

* The data given here refer to material collected in the experimental sediment-jars. The percentage of Foraminifera is a rough estimate based on a counting of fragments.

bacteria appear to play an important part in the layers of sand beneath the surface on the flat, which are everywhere more or less blackened, probably as a result of bacterial decomposition of the organic material present; and that the liberation of CO_2 by bacteria in the mud of the mangrove swamp may render that mud acid, thus causing some solution of calcareous material with which it may come in contact.

SPONGES.

The sponge fauna is rich and interesting, and includes not only surface-living forms and typical inhabitants of pools, but also a variety of encrusting species found under slabs and boulders. The presence of the mangrove swamp provides an unusual habitat for sponges, which grow upon the roots of the *Rhizophora*, and some of which are able to penetrate the more watery parts of the swamp. Some indication has already been given (pp. 38—39) of the species which are able to flourish in the vicinity of mangroves, but a more detailed study of this question should provide results of considerable ecological interest. The only sponge of commercial value is *Euspongia irregularis* var. *pertusa*, which occurs particularly in the mangrove park. This variety is closely allied to certain West Indian forms and has been recorded from the West Indies by Hyatt, but the identification is doubtful. It is in all probability a form peculiar to Australia, if any real distinction can be made between the races of *E. irregularis*. This sponge formed the subject of experimental work by F. W. Moorhouse, described elsewhere. Another common sponge, *Spiraстрella purpurea*, is remarkable for the great variation of its forms of growth, and for the fact that one of its facies resembles a colony of *Favia* so closely, in general appearance, that it might be quoted as a case of "mimicry." It is also noteworthy that sponges of certain curious cyathiform and other types common on the Outer Barrier (species of *Phyllospongia*) appear to be absent from Low Isles.

COELENTERATA.

(1) *Hydrozoa*.—Not many species are represented, and only two are common on the flat—*Dynamena crisioides* and *Myrionema amboinense*. The life-history of the latter was studied by E. A. Fraser and is described elsewhere in this volume. The large hydroid *Aglaophenia cupressina*, which is one of the striking features of the Outer Barrier, is apparently absent from Low Isles. Species of *Millepora* are fairly common, but occur among other corals and do not form independent reefs.

(2) *Scyphozoa*.—*Cassiopaea andromeda* is the only form recorded from Low Isles as an intertidal species.

(3) *Anthozoa*.—(a) *Alcyonaria*.—These are abundant and well represented by species as well as by individuals, and often attain a large size or cover extensive areas. It is a notable fact that nearly all the alcyonaria collected belong to the order Alcyonacea. These, with the exception of *Tubipora* and *Heliopora*, are all more or less fleshy forms (Plate XVI). This feature seems to be a characteristic of the Queensland reefs, whereas on reefs of other types, those of Florida for instance, the alcyonarian fauna consists almost entirely of Gorgonians, which give a very different facies to the reef. This distinction is so well marked at Low Isles that only two species of Gorgonians (a *Juncella* and a *Melitodes*) could be found, and these were apparently confined to shaded and overhanging surfaces on the seaward slope and formed no part of the ordinary surface-fauna. *Tubipora*, which is common on some reef-flats (e. g. Batt Reef), is rare at Low

Isles ; but *Helipora* is common in the anchorage and elsewhere on the seaward slope. The alcyonaria of Low Isles, therefore, do not in the main add directly to the substance of the reef ; but through the intermediary of spicules, liberated at the time of their death, they must add very greatly to it. An interesting study of the rôle played by alcyonaria in reef-formation has been published by Cary (1918).

(b) *Ceriantharia*.—This group is represented, so far as we know, only by a single species of *Arachnanthus*, which occurs in sand.

(c) *Antipatharia*.—A species of *Eucirripates* is fairly common on overhanging surfaces on the seaward slope.

(d) *Zoanthinaria*.—These forms, which occupy so small a space in the shore fauna of an English coast, are fairly important at Low Isles. They do not compare with the alcyonaria and madreporaria in abundance either of species or of individuals, but constitute a reasonable percentage of the coelenterate fauna. Species of *Palythoa* are the bulkiest forms, and may clothe large areas of rock.

(e) *Actiniaria*.—The group is well represented by interesting species, but many of them are of occasional occurrence. They include several of those types, characteristic of the warmer seas, which specialize in frond-like developments of tentacles, disc, or body (Plate XX, fig. 1), and also a number of perfectly ordinary species. A remarkable feature is the abundance of individuals belonging to species of large size (*Stoichactis kenti*, Plate X, fig. 1, is often a foot or 18 in. across, and the less common *Gyrostoma ramsayi* probably considerably more), but here again small species are as common as large ones. Commensalism between anemones, fish and prawns has already been mentioned (p. 47), but there is also an association fairly often seen between hermit crabs and *Calliactis miriam*.

(f) *Madreporaria*.—These are the dominant forms of life at suitable levels in the anchorage and on the seaward slopes. Certain species are able to flourish in the moats.

CTENOPHORA.

The only littoral form found at Low Isles was a species of *Coeloplana* taken from an alcyonarian in one of the moats.

TURBELLARIA.

Turbellaria of several species, including large and brightly coloured forms, are not uncommon under boulders and shingle, and form part of the fauna of the outer rampart. They may also be found among the beach sandstone.

NEMERTINEA.

We did not find many nemertines. The species most commonly found was a white one with longitudinal black stripes, allied to or identical with *Baseodiscus quinquelineatus*. Apart from this we can record only *Baseodiscus delineatus* and a species of *Lineus*.

ANNULATA.

(1) *Polychaeta*.—The most conspicuously abundant forms are *Spirobranchus gigantus*, which occurs especially in living blocks of *Porites* ; and the Polynoid *Iphione muricata*, which is common under boulders, etc. Several other species, including *Eurythoe complanata*, are more or less common, and some of these inhabit the sand. *Perinereis obfuscata* and *Platynereis polyscalma* are among the forms which may be caught by

attracting them to a light suspended over the water at night. The second of these species is a remarkable form, hitherto considered a rarity, but probably common at Low Isles. Luminous forms in great numbers were sometimes seen swimming near the cay at night, and these included *Odontosyllis hyalina* as well as the aforementioned *P. obfuscata*. Certain nereidiform species are to be found in the coral conglomerate of the inner rampart, in the crevices of the beach sandstone and the boulders, and in damp places under these. Although fairly plentiful and varied, the polychaets as a whole do not appear to be among the dominant groups, except in rocky crevices, the dead bases of corals, etc.

(2) *Oligochaeta*.—The occurrence of *Pontodrilus bermudensis* in the shingle-tongues of the mangrove swamp is an interesting record.

(3) *Gephyrea*.—It has already been indicated (pp. 56, 60) that Sipunculids are plentiful both in sand and rock. The number of species is considerable and that of individuals great.

CRUSTACEA.

(1) *Cirripedia*.—A comment on the occurrence of acorn-barnacles has already been made on p. 70; those collected all belong to the genus *Tetrachita*. Ships'-barnacles (*e.g.* *Lepas anatifera*) are sometimes washed ashore on logs, and an interesting boring species belonging to the genus *Lithotrya* forms an element in the fauna of the coral boulders.

(2) *Isopoda*.—Apart from *Ligia australiensis* (and perhaps other species similar to or associated with it), which is common on dry shingle, members of the group are not noticeably abundant. A certain number of forms (*e.g.* species of *Cymodoce*) occur under stones and in coral crevices, and it is probable that careful dissection of habitats such as the coral platforms in the moats, would reveal a considerable number more.

(3) *Amphipoda*.—Small species are locally abundant, for instance, under shingle. Species collected belong to the genera *Hyale*, *Ceradocus*, *Maera* and *Ampithoe*.

(4) *Decapoda*.—(a) *Natantia*.—These are poorly represented in our collections, because many of them belong to the fauna of commensals and crevice-living animals of the coral platforms and the living coral which, as explained in the preface, had to be omitted from our survey; but members of the group are of frequent occurrence. Two prawns (*Crangon strenuus* and *C. ventrosus*) are fairly common on the flat, and transparent species, often with opaque bands of cream and orange, are common as commensals with both coral and anemones. There are also small species living under boulders, and in the mangrove swamp. *Perichlimenes brevicarpalis* is one of the common commensals (with *Stoichactis* and *Thalassianthus*), and prawns similarly coloured were seen with living corals, including the species of *Fungia* with a tangle of tentacles 6 in. long, which remain expanded in daylight and form a refuge for the prawn. On one occasion, when diving in about 5 fathoms, a colony of *Euphyllia* some 2 ft. across was found, the coral being entirely hidden by a carpet of knobbed tentacles, among which were about two dozen of these prawns, of various sizes, all exhibiting the curious swaying motion, as if combing the tentacles, which is characteristic of them.

(b) *Palinura*.—*Panulirus versicolor* occurs in small caves and under overhanging rocks on the seaward slope below the level of low water.

(c) *Anomura*.—This group is represented by a moderate number of species, but some of them are very common. This applies particularly to some of the hermits (species of *Clibanarius*) and to the scuttling crab-like form *Petrolisthes lamarcki*.

(d) *Brachyura*.—The crabs form one of the most important elements in the fauna, including many species and innumerable individuals. They cover a wide range of form, and although they are naturally a mobile part of the population, some of them exhibit a considerable degree of response to environmental conditions, and arrange themselves distinctively with relation to the available habitats. Many of the commonest crabs belong to small and inconspicuous species, there being comparatively few large and showy forms. Their exoskeletons contribute a good deal of material to the sand of the reef. At least one species of *Cryptochirus* is of frequent occurrence in living colonies of *Favia* and *Symphyllia*.

(5) *Stomatopoda*.—Two species at least (*Gonodactylus chiragra* and *Lysiosquilla maculata*) are common, and there are other less plentiful forms.

ARACHNIDA.

The presence of a definitely marine spider (*Desis crosslandi*) on the flat is of interest. It occurs on the Thalamita flat and elsewhere, and is seen when slabs or boulders are turned over; in the crevices of these it makes a nest of fine mesh. It is undoubtedly submerged at high water. This species is hitherto recorded only from Zanzibar.

MOLLUSCA.

(1) *Amphineura*.—The Amphineuran fauna of Low Isles contrasts sharply with that of a region such as Sydney harbour. At Low Isles the number of species is small, but at least two are common, and the large *Acanthozostera gemmata* is astonishingly abundant. In Sydney harbour some 34 species belonging to 15 genera have been taken.

(2) *Gastropoda*.—The outstanding facts here are the large number of species, the vast quantity of individuals, and the great variety of conditions to which given forms have become adapted. The zonation of some of the species on the beach sandstone and the ramparts would repay detailed study, which we were unable to give to it. The gastropod fauna, far from consisting mainly of the large and brightly coloured shells so familiar in collections, consists primarily of small forms, whose shells are often dull in colour and inconspicuous, but some of which occur in countless numbers. The striking forms, though not in the majority, are nevertheless fairly well represented by certain of the larger species of cowrie (*Cypraea* and *Ovula*) and *Conus*; by the huge baler-shell (*Melo diadema*, Plate XXI, fig. 3); and by species of *Haliotis*, *Terebra*, etc. The Euthyneura include *Onchidium* in great quantity; nudibranchs of various species (among them a swimming form of magnificent coloration); a large and fairly plentiful aplysia; and the "ink-fish" *Dolabella scapula*.

(3) *Lamellibranchia*.—Here again species are numerous and individuals innumerable, and the fauna markedly subdivided among the several habitats. The boring forms (*Lithophaga*, *Gastrochaena*, *Tridacna crocea*, etc.) are among the actively destructive agencies on the reef; but some of the species, particularly the clams (*Tridacna* and *Hippopus*) are to be reckoned amongst the important suppliers of reef materials of coarse grade, since they are not only large, but also extraordinarily numerous, accounting for a colossal deposition of calcareous material from the sea-water.

(4) *Cephalopoda*.—Octopods were seen occasionally on the flat, some of them inhabiting lairs in coral debris. Squids (e.g. species of *Sepioteuthis*) were also of casual occurrence, and the shells of *Nautilus* and *Spirula* were among the shore-debris of the cay and of the adjacent mainland.

ECHINODERMATA.

The echinoderms are well represented on the reef. Considered as a unit in reef economy they make a considerable demand upon the plant, animal and detrital food supply. They are significant also as local movers and refiners of sediment, as suppliers of abundant organic material in the form of faeces, and of skeletal material which becomes part of the sand. In this rôle they are the more effective in that they are mostly animals of a large grade of size, as well as being represented by numerous individuals.

(1) *Asteroidea*.—Of the Asteroids two species whose adults live exposed to full sunlight are common—the vivid blue *Linckia laevigata* (Plate X, fig. 2) and a similar but less plentiful brown and yellow starfish, *Nardoa pauciforis*; whilst a third exposed species, the cushion-like *Culcita novae-guineae*, is also of somewhat less frequent occurrence. Of species which habitually conceal themselves, the most notable are *Asterina* (*Patiriella*) *exigua*, which is of universal prevalence under shingle fragments and in similar places, and *Archaster typicus*, a straw-coloured starfish which lives in the Sand flat and similar areas, and may be seen in numbers moving just below or flush with the surface as the flowing tide covers the flat. The distribution of *Asterina exigua* is distinctive in that it is a typical inhabitant of the shingly areas, occurring in countless numbers on the rampart.

(2) *Echinoidea*.—Of the Echinoids the most conspicuous are the magnificent *Centurchinus* (*Diadema*) *setosus* (Plate XX, fig. 2) and the large echinus-like *Triploneustes gratilla*; these two between them must account for the consumption of a great bulk of vegetable matter, and be a fruitful source of finely divided organic material extruded as waste. Much more plentiful than either, however, is the smaller urchin of varied coloration, *Echinometra mathaei* (Plate X, fig. 3), which is, according to Clark, probably the commonest sea-urchin in the world, and is a notorious borer; on the Outer Barrier we found it in the solid rock of the outer-moat floor.

(3) *Ophiuroidea*.—The *Ophiuroidea* are represented by several common species of somewhat different habits. Under boulders and in crevices of honeycomb-rock, especially on the flat, are to be found innumerable examples of *Ophiothrix longipeda*, a tabby-coloured species with arms which, in large specimens, may attain more than 2 ft. in length. This well-known Barrier Reef species is commonly associated with the salmon-tentacled lamellibranch *Lima tenera*. The association is not invariable (*Ophiothrix* being found frequently without *Lima*, though probably the reverse is not the case), but occurs sufficiently often to force itself upon one's notice. In the areas of honeycomb-rock, specially towards the south-east, and in the rocky-floored pools of the inner rampart, a characteristic element in the fauna is the black or dark-coloured *Ophiocoma scolopendrina*, which hides its body in an inaccessible cranny and trails some of its arms abroad. The restriction of the bulk of the population of this species (although individuals do occur under loose boulders, etc.) to areas of more or less solid rock at relatively high levels is interesting, and has been commented on by Clark with reference to its occurrence at Maer. The habitat of *O. scolopendrina* at Low Isles differs from its counterpart at Maer in that much of the rocky floor is covered by shallow water at all states of the tide; at Maer, where this is not the case, the trailing arms are withdrawn at low water. *O. longipeda* has a much more catholic distribution, and does not, in our experience, tend to trail its arms at low water, but we have seen it do so when covered by the tide.

(4) *Crinoidea*.—The echinoderm fauna of Low Isles has the interesting peculiarity that it includes no abundant Crinoid fauna between ordinary tide-marks. Clark records

the fact that on parts of the Maer Island reef (Torres Strait) Comatulids are very conspicuous and abundant, and that 21 species were found there by the Carnegie Expedition of 1913. It is not intended to state that no Crinoids can be found between tide-marks at Low Isles; a diligent search would no doubt provide a certain number of specimens; but there is no considerable population of them as at Maer, although they occur fairly freely below low water of ordinary spring tides. This state of affairs may be connected with the contrast which exists between the fauna of a reef such as Low Isles and that of reefs near or belonging to the Outer Barrier series (with which Maer ranks).

(5) *Holothuroidea*.—These are abundant, and include a number of species. Many of them fulfil an earthworm-like function in the shifting of reef-sediments. They are forms notoriously prevalent on coral reefs, and affect a variety of habitats, sometimes changing them with age, as, indeed, is the case with certain echinoderms of other groups. *Holothuria leucospilota*, for instance, lies free and exposed to direct sunlight when adult; but when young it appears to prefer sheltered shady places and may be found under the shingle of the rampart. Of the species which live in sheltered places when adult, some live under boulders and others in sand, a variety of small and young forms occurring under the shingle of the rampart. It has recently been shown by Baker (1929) that on a reef which he visited in the New Hebrides, certain Holothurians exhibit a very distinct zonation.

POLYZOA.

These appear to be rather poorly represented in the Low Isles fauna, being less abundant than on many temperate shores. The most interesting form is the finely branched coral-like species *Retepora graeffei*.

BRACHIOPODA.

So far as we are aware these are absent from Low Isles; but a species of *Lingula* is very plentiful in Mission Bay, Cape Grafton on the mainland some 35 miles to the southward.

ASCIDIACEA.

The ascidian fauna is curious in that individuals belonging to simple species were rarely seen. Compound ascidians, on the other hand, are very abundant, though in individuals rather than in species. The vivid blue or green *Diplosoma virens* is very widespread, and sometimes present in countless numbers. The white *Didemnum candidum* and a pink form probably belonging to the same species are also very common in a variety of places, and another species of this genus (*D. psammotodes* var. *skeati*) is fairly plentiful.

ENTEROPNEUSTA.

Only the two species mentioned previously (p. 56) were found, but both of these are abundant. Enteropneusts appear to form a characteristic element in the fauna of coral reefs, amongst which they are widely distributed. An interesting comment on them is made, for instance, by Gardiner in his reports on the Maldivé and Laccadive Archipelagoes (vol. i, pp. 47, 340).

FISHES.

A short account of the Low Isles fishes has been published by G. P. Whitley (1929).

On the reef flat several fish of moderate size are common. One is a very sleepy dog-fish, easily captured, and with large eye-like markings on its sides (*Chiloscyllium ocellatum*). Another is a handsome sting-ray, reddish brown with bright blue spots (*Taeniura lymma halgani*). A dark grey ray (*Himantura granulata*) occurs in the mangrove swamp. A really dangerous inhabitant of the reef, the stonefish *Synanceja horrida*, was taken on several occasions. A toadfish (*Tetrodon hispidus*) is fairly common, and a coffer-fish less so. Of the smaller fish, shoals are of frequent occurrence in moats (e. g. *Pranesus ogilbyi*), or around mangrove-roots (e. g. *Pseudomugil signifer*), and a number of species are commensal with coral. Of the large off-shore fish the mackerel-like *Scomberomorus commerson* is one of the local food-fishes. Sharks of large size (8–12 ft.) are apparently not very plentiful about the reef, though seen from time to time. They sometimes came very close inshore, and might be found, for instance, in the mangrove park at a state of the tide which hardly provided them with sufficient depth of water for movement. Rays of large size were sometimes seen leaping from the water near the shore, but close views of such species were obtained only on Batt reef, where they measured as much as 6 or 8 ft. across. Whitley states that the fishes of the mangrove area are, broadly speaking, “of an entirely different faunal facies from the coral fishes.” A note on the coral fishes will be found on p. 66.

REPTILES.

Geckos live on the cay and in parts of the mangrove swamp. Sea snakes were sometimes seen both on the reef flat and out at sea, but were not common.

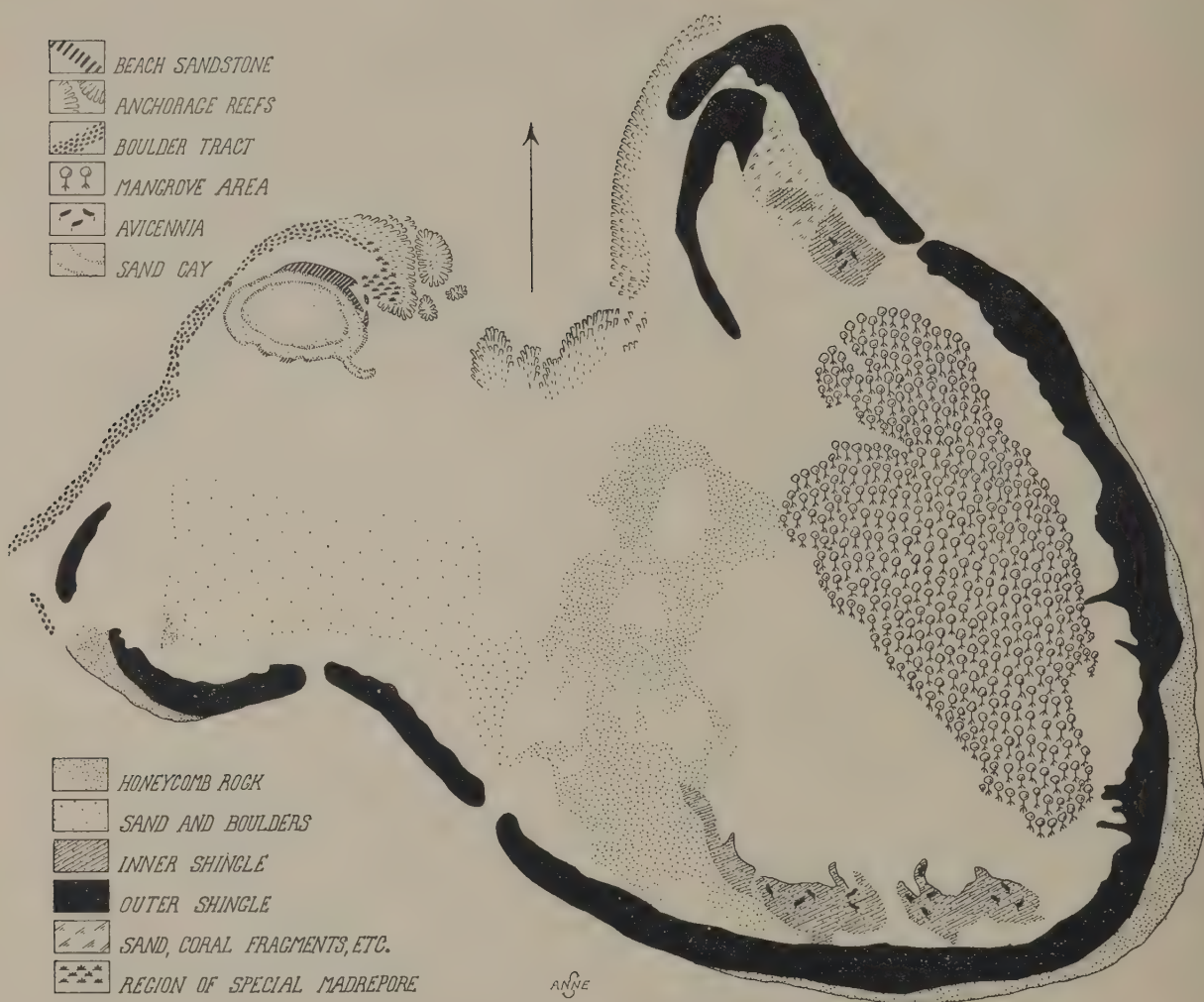
BIRDS.

The Low Isles reef is the territory of a pair of sea eagles (probably *Cuncuma leucogaster*), which nest in a tall tree in the mangrove swamp. The swamp is also the roosting-place of innumerable Torres Strait pigeons (*Myristicivora bicolor* subspecies *spilorrhoea*) during certain months of the year, and many of these fly to the mainland each day and to Low Isles each night. Grey and white herons (probably *Demigretta sacra*) frequent the reef, and many of these fly out to Batt Reef as the tide ebbs, arriving there as it begins to uncover. The cay is inhabited by other smaller birds, and migrants are sometimes killed by collision with the lighthouse.

ORIGIN OF THE LOW ISLES FAUNA.

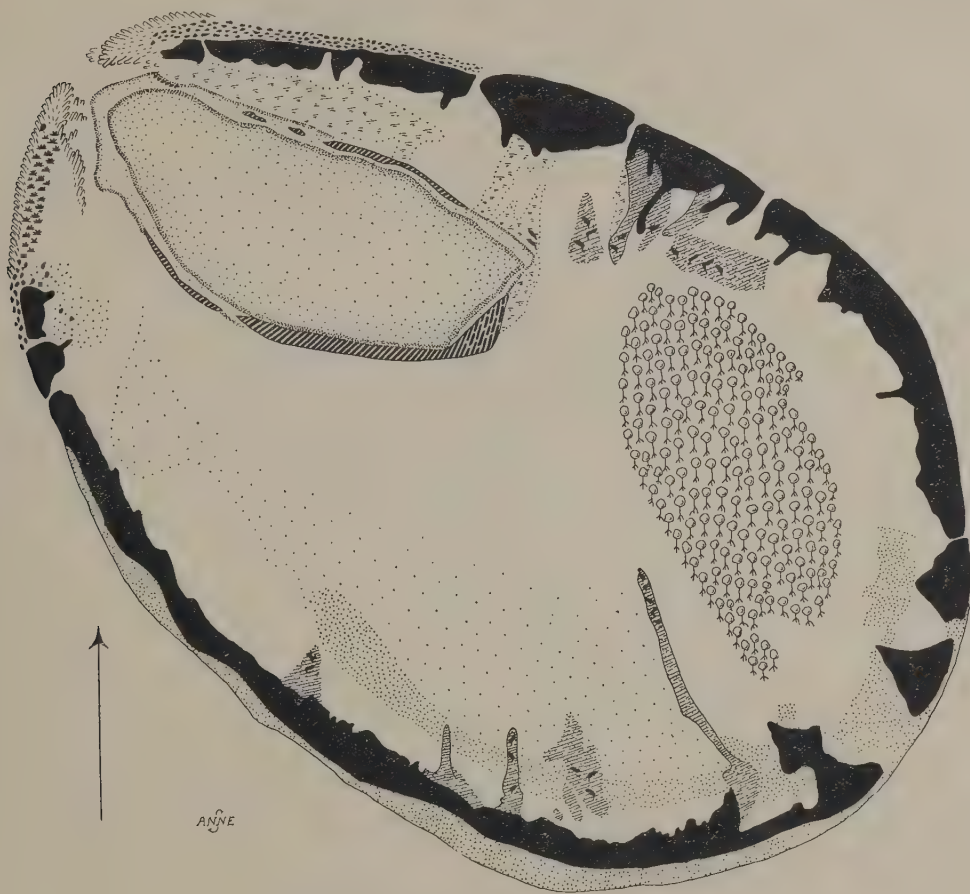
We hoped to make an analysis of the species represented in the Low Isles fauna, tabulating their known geographical distribution so that some idea of the composition and origin of the fauna might be gained. Since the species collected number many hundreds, this has proved too great an undertaking, and has been abandoned. It is possible, however, to give one illustration which will give an indication of the state of affairs, and which would probably prove to be of wide application.

The echinoderms of Low Isles include a number of more or less common representatives not yet mentioned in this report, some of which, though not particularly prevalent at Low Isles, are common elsewhere in the Barrier region; these include *Asterope carinifera*, *Echinaster luzonicus*, *Oreaster nodosus*, *Iconaster longimanus*, *Ophiarthrum pictum*, *Ophiolepis superba*, *Ophiocoma brevipes* var. *variegata*, *Ophiarachnella gorgonia*, *Ophiactis savignyi* and *Holothuria marmorata*.



TEXT-FIG. 12.—Diagrammatic analysis of the Low Isles reef, for comparison with the Three Isles reef, as represented in Text-fig. 13. The conventions used in the two figures are the same. The figures are an attempt to compare those areas in the two reefs which correspond ecologically; the terms used are therefore not necessarily intended to imply *morphological* correspondence between the parts compared, although a good deal of such correspondence is involved. Regions not strictly comparable ecologically are omitted; some of these are compared in Text-fig. 15. The mangrove area is represented by a uniform convention in both figures, as a guide to the eye; actually it contains glades and shingle tongues in both cases, but since the details of these are not known for Three Isles, the two reefs cannot be compared in this sense. The details for Low Isles are shown in Plate I.

If we take the species just enumerated, and add them to those mentioned elsewhere in this report, we obtain a series from which 33 species may be chosen to represent the echinoderm fauna of Low Isles. The existence of Lyman Clark's lucid and excellent monograph on the Echinoderm Fauna of Torres Strait makes it possible to analyse this group of species. Of the total of 33, 23 at least (probably more) are Indo-Pacific forms of



TEXT-FIG. 13.—Diagrammatic analysis of the Three Isles reef for comparison with Text-fig. 12.

greater or lesser range, whilst 6 belong to the East Indies, the Pacific, or both. One at least, probably two, are pan-tropical. Further, 8 of them are species listed by Clark as forms of very wide range, 5 as species of tropical Australian range, 4 as particularly characteristic of the Thursday Island area, and 14 as characteristic of the Barrier Reef area (the echinoderm fauna of which is in the main markedly different from that of the Thursday Island region). Clearly, then, the Low Isles fauna is predominantly Indo-Pacific as regards its echinoderms, and this undoubtedly applies in other groups, if not generally.

COMPARISON OF THE ECOLOGY OF OTHER REEFS WITH THAT OF LOW ISLES.

(By T. A. and ANNE STEPHENSON.)

I. THREE ISLES.

(Text-figs. 13-15 ; Plates II and XXII ; Plate XXVI, fig. 1.)

The survey of this reef was carried out by M. A. Spender and Anne Stephenson. The biology was studied by J. S. Colman, T. Iredale and T. A. Stephenson. The time thus occupied was a week, at the period of new-moon spring tides, in May, 1929. The survey, though brief, came towards the end of our careful study of Low Isles, so that we were able to make a satisfactory comparison in a short time.

Our notes on the physiography, fauna and flora of Three Isles are of considerable bulk, but there is no need to publish them *in extenso*, since the principal fact which they demonstrate is a very close similarity between Three Isles and Low Isles. A brief account of the structure of Three Isles (p. 27) has already been given, and this, together with the coloured maps and Text-figs. 12 to 15, bring out the points of resemblance and of contrast between the two reefs. It remains, therefore, only to mention certain features of particular interest connected with Three Isles.

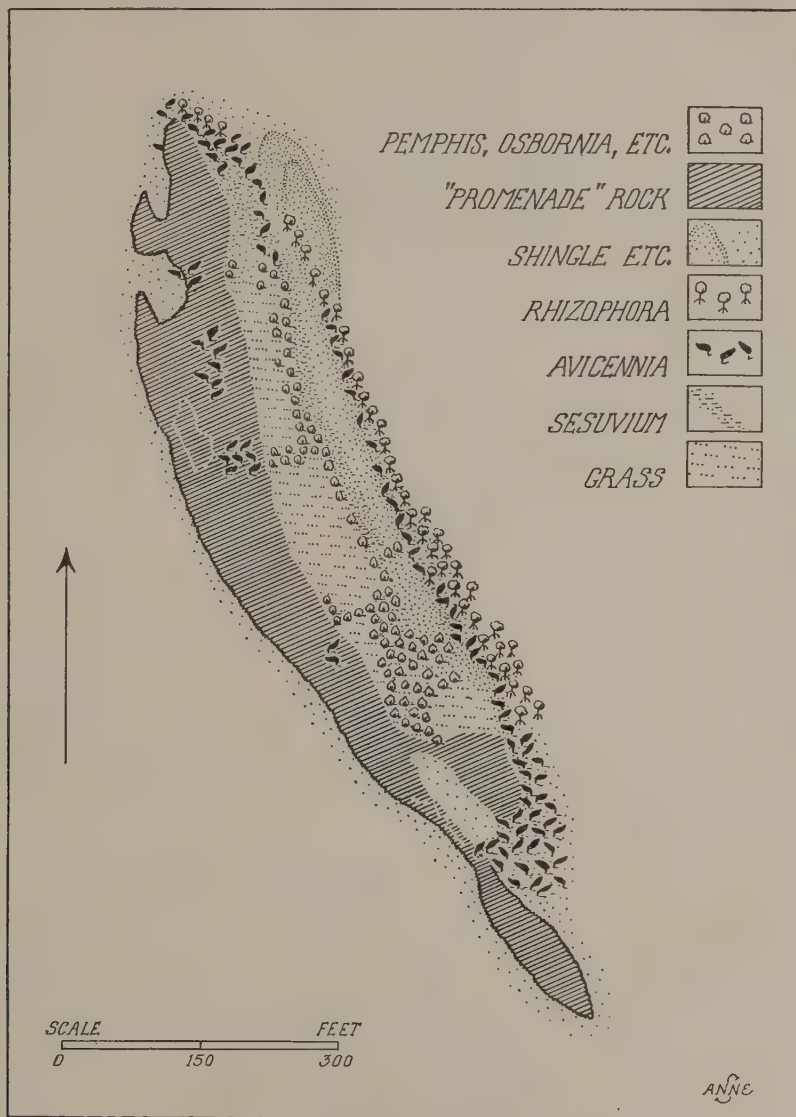
The ecological associations of Three Isles are exactly similar in principle to those of Low Isles. A complete list of species from Three Isles would be a question of repeating the Low Isles list, with a certain proportion of alterations. An extensive list is available only in the case of the mollusca (to be reported upon by Iredale), but numerous shorter lists compiled in the field show the same common organisms as at Low Isles. Some *differences* are as follows :

THE CAY.—The flora of the Three Isles cay probably gives a better idea of the flora characteristic of cays than that of the Low Isles cay, since it is not inhabited by light-keepers. Much of it had been burnt off previous to our visit ; but it includes a number of interesting species, notably the beautiful pink-flowered *Josephinia grandiflora*, a form typical of such situations, which was represented in the collections made by Banks at Lizard Island in 1770 and by Macgillivray at Three Isles in 1848. The trees are *Pandanus*, *Cocos*, *Casuarina*, *Terminalia*, etc.

There is more beach sandstone round the cay at Three Isles than at Low Isles, and it has an interesting zonation of molluscan species. According to Iredale the following species occur on all the patches of sandstone. The zonation from above downwards runs—*Melarhaphe coccinea*, *Tectarius malaccanus*, *Melarhaphe undulata*, *Planaxis sulcatus*, *Siphonaria*. Four species of *Nerita* (*chamaeleon*, *polita*, *plicata*, *albicilla*) occur without distinct arrangement throughout the above zones.

THE FLAT.—Three Isles has no mangrove park. Between the mangrove swamp and the very long shingle-spit outside its western border lies an interesting pool containing flat-topped platforms of massive corals (*Porites*, *Favia*, *Symphyllia*), together with

some platforms of *Heliopora* and *Pavona*, and a thoroughly interesting population of other creatures. This pool is rather similar to the "Porites pond" of Low Isles, and its



TEXT-FIG. 14.—Diagrammatic representation of the Third Island at Three Isles, showing the general distribution of zones of vegetation upon it.

population is that of a well-stocked moat. The flat just outside the swamp, to the north of this pool, is mostly sandy, with a thin colonization of *Thalassia*.

The tiger-cowrie (*Cypraea tigris*) is very common on the flat at Three Isles. This was probably equally common at Low Isles in the past, but has been so much sought after by lighthouse-keepers and visitors that it is now scarce.

CASUARINA SPIT AND THE DUNE present an interesting flora. Casuarina spit is covered by a coppice, including a variety of shrubs and flowering plants apart from the casuarinas. The dune (Plate XXII, fig. 3) varies from place to place; part of it is covered by woodland, part by vegetation somewhat resembling that of heath-country. *Pandanus* is among the trees of the area.

THE THIRD ISLAND (Text-fig. 14; Plate XXVI, fig. 1) gives an interesting example of plant-zonation. Its bands of shingle and debris are colonized by *Sesuvium*, grass, *Pemphis acidula*, *Osbornia octodonta*, etc.; along its eastern margin lies a belt of *Avicennia*, and between this and the flat a strip of *Rhizophora*.

THE PROMENADES (Plate XXII, figs. 1 and 2) have a fauna and flora of their own, distinctive features of which are the crab *Grapsus strigosus*, which clatters about the rocks; and the periwinkles *Nerita plicata* and *costata*. There is *Sesuvium* on top of the high promenade outside the mangrove swamp, among other places.

THE ANCHORAGE AND ADJACENT REGIONS.—A finishing touch is given to the ecological correspondence between Three Isles and Low Isles by the arrangement of areas in the anchorage. At Three Isles there is an area of slightly higher level than the rest (corresponding to the area A1 at Low Isles, described on p. 62), on which *Acropora pulchra* is conspicuous. The other anchorage reefs have a fauna comparable to that of A2, etc., at Low Isles. These points are indicated in Text-figs. 12 and 13.* The growth of coral in the Three Isles anchorage is particularly clean and fresh, and in May, 1929, was not at all infested by Cyanophycean beards, such as were smothering the Low Isles coral at the same time.

A region at Three Isles which has no exact counterpart at Low Isles is to be found between the anchorage and the flat. It is like a much more extensive version of the small area at Low Isles where the northern moat opens on to the anchorage. It is a wide stretch of pools and platforms of *Acropora*, massive *Porites* and *Montipora ramosa*, supporting a rich fauna, and intermediate in its conditions of life between a moat and the anchorage—a moat-like area more directly in contact with the open sea and, when not submerged, with water continually streaming through it.

Only one common coral species was noted as a form not familiar to us at Low Isles. This was an important form ecologically—a species of *Acropora* (*A. brueggemanni*) occurring in quantity on the part of the flat adjacent to the anchorage, and making platforms like those of *A. hebes* at Low Isles (the latter species was also present).

Certain alcyonaria are common in the anchorage which are not recorded from Low Isles—these include *Isis hippuris*, *Cespitularia multipinnata*, and another species of *Cespitularia*.

II. YONGE REEF.

(Text-fig. 5; Plate XVII, fig. 2; Plates XXIII and XXIV; Plate XXVI, fig. 4.)

During the new-moon tides of June, 1929, we established a base on Lizard Island, and from there Yonge Reef was visited on five successive days. A short visit was also paid to Ribbon Reef on 4th June. These two reefs have been named since our visit: the name Yonge Reef was proposed by the Admiralty; the name Ribbon Reef was suggested by us and confirmed by the Admiralty. The work on Yonge Reef was carried out by M. A. Spender, Anne Stephenson, E. A. Fraser, S. M. Manton and T. A. Stephenson. An instrumental survey was not possible in this case.

* *Acropora pulchra* occurs in the areas marked "region of special madreporæ," in these figures.

In the fauna and flora of Yonge Reef we were presented with a new set of problems, offering very little basis for comparison with Low Isles and Three Isles. The coral and alcyonarian species were unlike those with which we had become familiar, and although closer study showed that many of them represented modified growth-forms of Low Isles species, or forms which in the latter place are limited to the windward side, others were actually new, and everything looked a little different. This, I believe, is a common experience in turning from one reef to another, but it is important and worth careful investigation, because a solution of the problem presented would go a long way towards elucidating the distribution and evolution of marine species in general. It is probably only partly correlated with the differences in environment between one reef and another.

At Yonge Reef the complications presented by the occurrence of ramparts, mangroves, and a sandy reef-flat, do not exist. In their place the question of the relationship of organisms to Pacific breakers becomes insistent; and there are new factors involved in connection with the curious series of band-like zones already described (p. 32) which make up the seaward side of the reef. The meaning of the exact configuration of these zones it is impossible to interpret accurately in the present state of our knowledge. We can therefore only describe the life of the zones, and leave the interpretation to the future. The description starts at the Pacific border and works inwards.

THE OUTER RIDGE (Plate XXIII, fig. 2).—Coral grows luxuriantly on this ridge.† The corals include massive species, some of them growing to large size, and species of *Acropora* of certain styles of growth. These latter may form wide dish-like brackets or expansions (*A. hyacinthus*), encrusting sheets yards in extent (*A. palifera*), systems of heavy branches closely applied to the substratum (*A. decipiens*); or may consist of very short massive cones united to a firm foundation (*A. gemmifera*). Apart from these more or less solid forms, a totally different species (*A. delicatula*), occurring particularly on the sides of clefts, makes small rounded bushes of branches so slender and brittle that an entire specimen can with difficulty be obtained—yet this form can withstand the breakers.*

THE OUTER MOAT (Plate XXIII, fig. 1).—The coral here is most profuse near the outer ridge, where it occurs on large rocky prominences intersected by deep pools and crevasses. Little of this becomes fully exposed even at low water, and the water of the moat is normally agitated; it can rarely, if ever, approach the still conditions of a moat at Low Isles. The corals include the several growth-forms already mentioned for the outer ridge, and a variety of others beside. Conspicuous organisms other than corals are a large and handsome yellowish-brown hydroid (*Aglaophenia cupressina*), which is notably abundant, a common sponge of Heliopora-like growth (*Phyllospongia ridleyi*), *Spirobranchus giganteus* buried in coral, and various alcyonaria. There are also clams, gastropods, hermits, compound ascidians and encrusting sponges. As the water becomes shallower towards the reef-crest the floor becomes smooth, the coral more and more scattered, and the sea-urchins *Echinostrephus molare* and *Echinometra mathaei*, abundant. Both are borers, the former making deep rounded holes, sometimes as many as six to the square foot.

A primary feature of Yonge Reef is the heavy incrustation of nullipores. Even the

* The well-known views of Wood-Jones on the relationship between growth-form and environment in corals will be discussed in another paper.

† The upper part of the actual Pacific slope of the reef also appears to support a rich growth of living coral, since the refracted image of such a growth can be seen in the arch of the breakers before they disintegrate.

gastropods are usually overgrown by them. All the zones from the Pacific to the boulder zone consist of solid rock swept clear of loose debris, and for the most part so generally encrusted with nullipores that the prevailing colour of the substratum is a purplish pink. This is misleading, because the rock consists of coral and the nullipores are only a veneer; but it renders the landscape to leeward incomparably beautiful, for it has a pink foreground, with the brilliant blues and greens of shallow water over white sand behind it. A factor of importance connected with Yonge Reef is that the floor of its leeward side consists of very clean, rather coarse white sand. No mud or greyish sand, like that of Low Isles, was seen, and the water is very clear.

THE REEF CREST (Plate XXIII, figs. 1, 3 and 4).—This slopes upward from the outer moat to a summit-zone. Species of *Acropora* dominate, including *A. hebes*, *pulchra squamosa* and *gemmifera*. The two former make low bushy growths, the latter cyathiform structures with a stout stalk and short branches on top. *A. gemmifera* is particularly characteristic of Yonge Reef, and has short branches, which exhibit varying degrees of reduction to thumb-like or conical processes (Plate XXIV, fig. 2). Besides these are corals belonging to other genera, together with alcyonaria (including *Tubipora* as well as soft forms) and other organisms. Among the latter the most conspicuous are *Aglaophenia cupressina* and *Linckia guildingii*, the latter being a fawn-coloured starfish similar to the blue *L. laevigata* of Low Isles, which is also present. *Phyllospongia ridleyi* and a grey-green Zoanthid are also very common here. Where boulders occur there is a good growth of underside sponges, compound ascidians (including *Chorizocarpa sydneyensis*), small spider-crabs, oysters, *Sertularia*, etc. In shallow pools a squilla is common, and clams, gastropods, hermits, *Palythoa*, *Stichopus chloronotus* and other holothurians are present. A characteristic alga is *Chlorodesmis comosa*, and there are small amounts of *Halimeda* and *Caulerpa*.

The reef-crest varies to some extent from one place to another. In many places (Plate XXIII, fig. 3) it is very bare, in others (Plate XXIII, fig. 4) there is a considerable growth of coral of a certain type. The dominant species of *Acropora* vary to some extent. *A. gemmifera* is usually plentiful; sometimes patches of *A. hebes* and *pulchra* occur; elsewhere *A. squamosa* becomes dominant. At its northern end the reef-crest loses height and fans out, becoming covered by a good growth of *Favias*. At the southern end it also slopes downward, and terminates in a peculiarly bare zone with a poor growth of *Melobesieae*, but with a turf of soft algae; there is hardly any coral here. The reef-crest appears to have caverns beneath it, since water wells up through holes in its surface.

Connected with the ends of the reef-crest are some curious areas (Text-fig. 5), which present variations upon the zonation of the principal length of the reef, as follows:

A. *Madrepore Fields*.—Immediately to westward of the southern termination of the reef-crest lies an area (Plate XXVI, fig. 4) covered by a luxuriant growth of *Acropora hebes*. *Acropora gemmifera* is a subsidiary form here, and other corals are present in smaller numbers. At the northern end of the reef is a second field of *A. hebes*, this time to seaward of the end of the reef-crest; and there the branches of the madrepores are shorter and thicker than in the southern field.

B. *Intermediate Zones*.—At the southern end of the reef there are curious areas, lower in level than the reef-crest, and situated to seaward of it, in which the floor is horizontal instead of sloping. A similar area occurs at the northern end.

THE INNER MOAT (Plate XXIII, fig. 4).—Here the bottom is still rocky, but

irregular, and such boulders as occur are mostly cemented to the floor. Coral growth is fairly strong, often in scattered clumps. The fauna and flora reflect those of the outer moat, but the general effect is often somewhat impoverished. The inner moat is well marked in places, but sometimes, and perhaps over considerable stretches, the transition from reef-crest to boulder zone is gradual, a distinct moat being absent. This occurs notably in two areas of rather distinctive character, one at either end of the reef, which are labelled "sub-terminal areas" in Text-fig. 5.

THE BOULDER ZONE (Plate XXIII, fig. 4).—Here for the first time loose boulders and other debris are encountered in some quantity, and sand also appears in certain of the pools. Corals are scattered about the rocks and in the pools, and are similar to those of the inner moat, though somewhat less frequent. There is a good fauna beneath the boulders. There are also thick patches of *Caulerpa* and *Halimeda*, a great deal of *Spirobranchus* in the coral, some clams (*T. crocea* and *T. fossor*), *Linckia laevigata* and *gouldingii*, *Echinometra mathaei*, etc. At the southern end of the reef an expansion of the boulder zone ("southern boulder area" of Text-fig. 5) comes into contact with the outer moat.

THE ANCHORAGE CORAL ZONE.—This zone has been so named because it resembles, both in structure and fauna, the reefs found in the anchorage at Low Isles. The association of corals which grow on the leeward sides of reefs in the shallower water, on the tops and sides of rugged masses of rock with sandy pools between, constitutes a distinguishable series of species and growth-forms, to which we referred during our work as the "anchorage-coral" association. This community will be defined more closely in a later report, and will be contrasted with other groups characteristic of different habitats; for the moment it will be enough to say that it is distinct from the association characteristic of the windward slopes of reefs at comparable levels.

In this zone the blocks of dead coral are richly overgrown by living forms in great variety, amongst which stagshorns and other species of *Acropora* predominate. *Acropora palifera* is one of the common species, and this, under several growth-forms (some of which may be distinct species) is present in most parts of the reef. It is a massive, encrusting or lobed form unlike the other species of the genus. The pools abound in brightly coloured fish. In the deeps there often flourish great clumps of staghorn coral, directly on the sand, unsupported by any considerable piece of rock or other solid foundation. Among the coral are giant clams (*Tridacna derasa* and *T. elongata*), as well as the smaller species. *Hippopus* is present, but is scarce on this reef. There are also crinoids, and algae such as *Chlorodesmis* and *Halimeda*.

THE ZONE OF CORAL HEADS (Plate XXIV, fig. 2).—The coral heads, many of them very large, are mostly well spaced, with a sandy floor between them, bare but for odd boulders and patches of staghorn coral. Their tops emerge 2–3 ft. at low water of extreme tides, the average emergence being about 1 ft. Some of them are completely covered across the top by a very rich and dense growth of living coral; other have the tops partly dead, with loose shingle, etc. The incrustation of the dead parts with nullipores is very extensive, and these sometimes veneer large masses of coral, which appear to be made of solid nullipores until broken. The colour of these nullipores was often pure white; this probably means that they were dead. A very considerable proportion (some 10% to 20%) of the living corals exposed during this set of tides were killed by the sun, their clean white skeletons advertising the date of their death with some precision, since the skeleton becomes brown and encrusted within a few days of death. The dominant corals of the

tops of the coral-heads are species of *Acropora*, particularly bracket-like forms and species with short thick branches; but many other subsidiary species occur. The growth is well illustrated by Plate XXIV, fig. 2.

THE FAUNA AND FLORA OF THE REEF AS A WHOLE.—The following list of organisms will give some idea of the general population of the reef.

FAUNA AND FLORA OF YONGE REEF.

PORIFERA.

- Stelletta purpurea*.
- Phyllospongia foliascens*.
- „ *ridleyi*.
- Various other species, both surface and concealed forms.

HYDROZOA.

- Aglaophenia cypressina*.
- Sertularia*.
- Millepora*.

ALCYONARIA.

- Tubipora*.
- Xenia*.
- Sarcophytum*.
- Lobophytum*.
- Sinularia*.
- Heliopora*.
- Lithophytum arboreum*.
- „ *digitatum*.

ZOANTHINARIA.

- Palythoa* and other forms.

MADREPORARIA.

- Seriatopora*.
- Pocillopora*.
- Stylophora*.
- Euphyllia*.
- Cyphastrea*.
- Echinopora*.
- Galaxea*.
- Favia*.
- Platygyra*.
- Coeloria*.
- Hydnophora*.
- Symphyllia*.
- Lobophyllia*.
- Pavona*.
- Astreopora*.
- Montipora*.
- Acropora*.
- Goniopora*.
- Porites*.

POLYCHAETA.

- Spirobranchus giganteus*.

BRACHYURA.

- Charybdis orientalis*.
- Actaea tomentosa*.
- Zoymus aeneus*.
- Trapezia ferruginea*.
- „ (commensal with *Stylophora*).
- Percnon abbreviatus*.

GASTROPODA.

- Trochus*.
- Clava vertagus*.
- Cypraea lynx*.
- „ *moneta*.
- Pterocera*.
- Thais armigera*.
- Drupa cornus*.
- „ *ricinus*.
- „ *rubus-caesius*.
- Latirus smaragdulus*.
- Conus lividus*.
- „ *marmoreus*.
- „ *striatus*.
- „ *vexillum*.

LAMELLIBRANCHIA.

- Tridacna crocea*.
- „ *derasa*.
- „ *elongata*.
- „ *fossor*.
- Hippopus hippopus*.

ECHINODERMATA.

- Linckia guildingii*.
- „ *laevigata*.
- Nardoa pauciforis*.
- Echinometra mathaei*.
- Echinostrephus molare*.
- Stichopus chloronotus* and other *Holothurians*.
- Crinoids.

ASCIDIACEA.

- Chorizocarpa sydneyensis*.
- Botryllus magnicoecus*.

ALGAE.

- Caulerpa* and *Halimeda* present.
- Chlorodesmis comosa* abundant.
- Melobesieae* dominant.

III. LIZARD ISLAND.

(Text-fig. 6 ; Plate XXV ; Plate XXVI, fig. 3.)

We camped on this island from 1st to 12th June, 1929. On four of these days examinations were made of some of the reefs surrounding the island.

These reefs are not all of the same type. They form a curious series and would repay further study. In Text-fig. 6 the principal reef-areas are represented in solid black. From this figure it may be seen that a considerable part of the coast-line possesses a narrow band of fringing reef ; that a more extensive system of reefs occupies the space between Lizard Island and its southern satellites Newt and Iguana Islands ; and that in addition to these there are small reef-patches here and there. It may also be seen that a shoal flanks the western side of the system of islands.

THE FRINGING REEFS.—These are narrow band-like reefs adjacent to the coast. They are seen to advantage from the slopes of the mountain, their form, extent and abrupt seaward edges being clearly defined against the white sandy bottom. One of these reefs was examined. Inshore were a few granite boulders, with some coral debris and shingle partly masked by a dense growth of *Sarcophytum*, *Lobophytum* and *Simularia*. The water even inshore was about a foot deep at this tide (9th June), many of the alcyonaria projecting. Proceeding towards the edge of the reef the water deepens, and about 10–15 yards from the shore there are large masses of living *Porites*, frequently a couple of yards in diameter, with pools and channels between. These masses continue to the edge of the reef, which lies some 50 yards from the shore, and descends rapidly to deep water, in irregular steps ; and towards the margin the pools and crevices are of considerable depth. Outside the reef-edge the bottom is clean sand. On and between the larger coral masses flourishes a rich and varied growth of other corals and alcyonaria, including fields of *Simularia flexibilis*. This fauna resembles that described below (p. 88) for one of the isolated reef-patches, and includes, in addition to the forms there mentioned, species of *Oulophyllia*, *Tridacophyllia*, *Pachyseris*, *Pavona*, *Echinopora*, *Galaxea*, *Psammodora*, lobed and foliose *Porites* ; *Stichopus chloronotus* and *Gyrostoma ramsayi*.

This reef, which is probably typical of the fringing reefs of the island, appears to be a young reef, with no reef-flat, still narrow, and consisting mainly of living coral, with a predominance of massive *Porites*. The escarpment which forms the seaward face is made of tiers of living colonies of this coral.

THE REEF PATCHES.—The nature of the reefs other than straightforward fringing reefs is indicated in Plate XXV and Plate XXVI, fig. 3. Plate XXV represents the view to southward from a height of some 1100 ft. near the summit of Lizard Island. In the foreground the coast and foothills of the island are seen ; in the middle distance, the satellites, Newt and Iguana Islands ; and between these and the foreground, a system of reefs. Between Iguana and Newt Islands, and between the latter and Lizard Island, this reef-system has a distinct edge and constitutes a sort of miniature barrier-reef upon which there is surf in ordinary south-easterly weather. This barrier encloses a deep pool (to the left of the figure), a practicable anchorage for small craft, with an entry which lies just outside the picture. Westward of the pool, between Iguana and Lizard Islands, lies a sandy shoal of complicated outline and very variable in level. Upon this occur numerous reef-patches, some of them adjacent to the shore of one or other of the islands, others quite isolated. In Text-fig. 6 this latter area is represented very conventionally ;

the two black masses actually represent groups of reef-patches, and many individual patches are omitted. Some of the latter are shown in Plate XXVI, fig. 3. The sea floor to westward of Lizard Island, as far as the eye can see from the slopes of the mountain, is sandy, with isolated reef-patches, some of them at a considerable distance from the shore. The distant reefs in Plate XXV are not reef-patches, but are large reefs belonging to the "inner series"—Eagle Island, M Reef and L Reef. The relation of these to Lizard Island and to the mainland is indicated in Text-fig. 1.

Three of the isolated reef-patches were examined, and one of these (lying to the west of Iguana Island in Plate XXV) will be described. It is a reef separated by some distance from any shore, and surrounded on all sides by sand. The shape is roughly triangular, the apex to windward (S.E.). The reef is made of dead boulders and masses of coral with sand between, and the surface is very irregular and full of complex holes and crevices. The edges are abrupt, about 6 ft. deep on the windward side. The general surface of the reef (apart from exceptional prominences) was about a foot below the level of low water at the tide of 3rd June; at an extreme tide there would be some exposure.

The whole reef is covered with a rich and healthy growth of coral and alcyonaria, resembling that of the Low Isles anchorage, but including some elements characteristic of more exposed situations. Fleshy alcyonaria are plentiful; *Acropora* is represented by about twelve species, including *A. palifera* and cyathiform, stagshorn, and bush-like species; and *Montipora* by both branched and foliose forms. Among the corals are other creatures, especially giant clams, some of them 3 ft. long or more. The largest species is apparently identical with *T. derasa*, the other with *T. elongata*. Smaller species are also present. Further details of the fauna are given in the list at the foot of this page.

The interest of the reef lies in the picture which it presents of the structure and fauna of an isolated reef-patch growing up from a sandy floor. The conditions described probably resemble those which prevail on any comparable reef before it has acquired a reef-flat or a modified surface which restricts or abolishes the growth of coral on top of it. A second reef-patch which we examined, a little to westward of the one described, seemed to have reached a slightly more advanced condition, since it had a sort of embryonic reef-flat of boulders, sand and shingle, with a slight stony bank at one side, exposed at low water. Here the growth of living coral was restricted on top of the reef, but was very rich down the steep sides. Connected with this reef was a notable mass of coral many feet deep, square yards of which were covered by a living colony of *Diploastrea heliopora*.

FAUNA OF REEF-PATCH DESCRIBED ABOVE.

HYDROZOA.

Aglaophenia cupressina.

ALCYONARIA.

Sarcophytum.

Lobophytum.

Sinularia (*S. flexibilis* and other species).

Isis hippuris.

ZOANTHINARIA.

Palythoa.

MADREPORARIA.

Discosomidae.

Seriatopora.

Pocillopora.

MADREPORARIA—continued.

Stylophora.

Favia.

Platygyra.

Coeloria.

Symphyllia.

Lobophyllia.

Merulina.

Fungia.

Herpetolitha.

Polyphyllia.

Turbinaria (massive and foliose species).

Montipora.

MADREPORARIA—*continued*.

Aeropora.
Goniopora.
Porites (massive).

MOLLUSCA.

Tridacna crocea.
„ *derasa*.

MOLLUSCA—*continued*.

Tridacna elongata.
„ *fossor*.

ECHINODERMATA.

Linckia laevigata.
Echinometra mathaei.
Crinoids.

IV. BATT REEF.

(Text-fig. 4 ; Plate XXVI, fig. 2.)

This reef was visited on a number of occasions from Low Isles. The area best known to us is the north-western part of the reef, somewhat south of its northern extremity, and in one of the pools in this region a small area was surveyed in detail. Apart from this, some examination was made by Tandy across the northern end of the reef, and one long trip was made by several of us in a dinghy across the sand-flat and down the length of the reef, ending at a point on the seaward edge near the south-east corner. A landing was also made on a reef-patch between Batt Reef and Tongue Reef. Our knowledge of Batt Reef is summarized in Text-fig. 4.

The only primary growth of living coral to be found on this reef occurs on its seaward slopes. The reef-patch just mentioned bears a rich and flourishing coral fauna.

The enormous central sand-flat has its own internal fauna, but the surface is almost bare for miles. Passing over it in a dinghy just before or after the period of low water, one sees a great population of fish, including shoals of large species, and rays 6 or 8 ft. across. The surface of the sand is populated chiefly by sand-binding plants, amongst which species of *Caulerpa* often form trailers many yards in length. *Thalassia* and *Cymodocea* are also present. Here and there are isolated boulders or patches of reef, and scattered colonies of *Pocillopora bulbosa* are a characteristic feature. *Stoichactis* is common.

The regions of the reef between its margin and the central flat present a bewildering labyrinth of scattered patches of dead coral or boulders with sand between, the general appearance of which is illustrated in Plate XXVI, fig. 2. Among and upon the dead coral there is a secondary growth of living coral, including a considerable number of species, but usually of a scanty nature, save in the deeper pools, where it sometimes becomes fairly flourishing, though rarely comparable with an open-water growth. The population of reef-flat organisms other than corals is considerable and interesting, resembling in many ways that of an area such as the Thalamita flat at Low Isles, and varying from place to place according to whether the particular spot is exposed or not at low water. In some of the shallow areas, where there is a strong current during the ebb, conspicuous members of the fauna are curious cup-shaped and other sponges (*Phyllospongia foliascens*, etc.) and small colonies of *Tubipora*.

A small area situated on a reef-patch in one of the deeper pools was surveyed in detail. The substratum consisted of irregular masses of dead coral, with sand between ; only the tops of the masses were uncovered at extreme tides. Corals were represented by more than 70 colonies, most of them small, and there were 85 colonies of *Xenia umbellata*. A vivid blue form of the ascidian *Diplosoma virens* was abundant. The dead coral was much overgrown by short algae, including microphytic forms, and some of these were also epiphytic. The prominent algae of larger size were *Turbinaria ornata* and *Amphiroa*

fragilissima. The data are summarized in the following table. This represents the population of a typical area of coral growth of a scanty type.

Surface Population of an Area 6 feet 8 inches square on Batt Reef.

CORALS :		ALGAE :		OTHER ANIMALS :	
<i>Favia</i>	29 colonies.	<i>Turbinaria ornata</i>	42 stems.	<i>Xenia umbellata</i>	85 colonies.
<i>Porites</i>	20 "	<i>Amphiroa fragilissima</i>	—	<i>Diplosoma virens</i>	} Abundant.
<i>Pavona</i>	>10 "		69 countable tufts ; con-	<i>Orbitolites complanata</i>	
<i>Acropora</i>	5 "		siderable amount not	<i>Euspongia</i>	2 specimens
<i>Pocillopora</i>	2 "		countable.	<i>Aplysia</i>	1 specimen.
<i>Galaxea</i>	1 colony	<i>Melobesia</i>	Abundant.	<i>Nudibranch.</i>	1 "
<i>Goniopora</i>	1 "	<i>Dictyosphaeria</i>	} Present in small amounts.	<i>Tridacna fossor</i>	1 "
<i>Coeloria</i>	1 "	<i>Caulerpa</i>			
<i>Symphyllia</i>	1 "	<i>Bornetella</i>			
		<i>Halimeda</i>			
		<i>Galaxaura</i>			
		<i>Laurencia</i>			
		<i>Cyanophyceae</i>		<i>Echinometra mathaei</i>	1 "
				<i>Sedentary polychaet</i>	1 "

At the point visited near the south-east corner, the margin of the reef forms a smooth rocky pavement, with a very gradual slope, much overgrown by mossy algae, with scattered corals—Astraeids, creeping colonies of *Acropora decipiens*, and low massive colonies of *Pocillopora*. Behind this pavement lies a wilderness of pools and boulders, from which the transition to the central flat is gradual.

Batt Reef occupies a position at the junction of the Outer Barrier proper with the series of "inner" reefs ; but from an ecological point of view it may probably be reckoned as a member of the inner series. The general appearance of some of these large inner reefs, viewed from a height, is indicated in Plate XXV. The three here represented (Eagle Island, M Reef and L Reef) were not visited, but probably have much in common with Batt Reef.

V. OTHER REEFS.

The descriptions of the structure and natural history of reefs of several kinds, which have now been given, can claim no more than to furnish some idea of the variations in structure and ecology which replace one another and combine in diverse ways, over a section of the Great Barrier Reef lying between Trinity Opening and Cook's Passage. It has been indicated by Spender (1930) that this section of the great reef differs considerably from that part of it which lies south of Trinity Opening. In the northern section, where the reef has a definite edge (the Outer Barrier) descending steeply to beyond the 100-fathom line, those reefs which lie between this edge and the mainland appear to be differentiated into series ; a chain of "inner reefs" between mainland and outer barrier, separated from both by channels ; and a series of "island reefs" in the steamer-channel between the inner reefs and the shore (Text-fig. 1). We have so far aimed at a characterization of the ecology of these three kinds of reef, together with that of submerged reef-patches such as must have been antecedent to any of them. Should detailed accounts of reefs southward of Trinity Opening subsequently become available, it is possible that here different types will emerge, and that there will be a greater uniformity from one to another, or at least a less marked differentiation into series.

It is now time to make some comment upon coral reefs described in the literature of the subject but outside our own experience. We do not propose at present to make

any detailed comparison between the reefs described here and those described by others, but only to indicate one or two points of interest. The time for the full comparison is not yet. Two quotations will emphasize my meaning. First, Spender, in his paper in the *Geographical Journal*, vol. lxxvi, 1930, p. 290: "There is still a great deal of information to be obtained from the measurement and examination of the surface features of coral reefs; as more results become available comparisons perhaps more valuable than individual accounts will be possible. It seems that shallow boring, mapping, and levelling could with advantage be carried out to a considerable extent before another deep boring is made, and that a more complete knowledge of reef structures and reef processes is necessary before the world problem as expressed in such a phrase as "The Problem of Coral Reefs" can be adequately treated." Second: There are necessarily, at the present stage, many structures described in the existing accounts of coral reefs of which one can only say with Professor Sollas (*Funafuti Report*, p. 24), "I do not understand it, and forbear from speculation."

In the Queensland Barrier we are dealing with a series of reefs in which coral appears to play a greater part at the present time than it does in an atoll such as Funafuti. At the latter place the coral is fairly plentiful and varied in the lagoon (which has no exact counterpart in the Great Barrier region), but on the platform of rock forming the rim of the atoll it appears, on the whole, to be distinctly scanty, as is also the case on the uppermost part of the seaward slope. "Of coral there is less than ever, and where it does occur it is in small isolated pieces" (*Funafuti Report*, p. 130). On the Outer Barrier, by contrast, the seaward regions are rich in growing coral of great variety and bulk. Here, therefore, they must add more substance to the reef than do those of Funafuti; and although their transformation into reef rock is accomplished in both places by lichenous nullipores and similar agencies, the relative importance of the coral on the Great Barrier would appear to be greater. Another apparent contrast exists in the relatively greater importance of *Halimeda* at Funafuti than on the Great Barrier. Gardiner's description of Minikoi Atoll suggests that there the proportion of coral growth is intermediate between that of Funafuti and that of the Outer Barrier.

One of the keys which will be required before the multiple lock guarding the general problem of coral reefs can be expected to yield, will be a precise comparison of those pavements of coral rock which form the fringes of reefs where they face the surf. We possess already a number of good descriptions of these, but further data, together with a study of the conditions of organic life in these fringes, will be needed before we can feel certain of the ground. In the reefs of the Queensland Barrier described in this report the pavement occurs in two forms, but is present wherever the reef faces the waves raised by the south-east trade wind or the Pacific swell. In the case of the island reefs (Low Isles and Three Isles), where the waves experienced are not of the magnitude of Pacific breakers, and also along the southern shore of Batt Reef, the seaward fringe is a simple pavement of rock, sloping gradually into the waves, much felted by mossy algae, and supporting only a low and scattered growth of coral. On an Outer Barrier reef (reaching its best exemplification in the case of Yonge Reef) the rocky seaward part of the reef is very wide; the pavement of the reef-crest lies at some distance from the breakers, and from it the seaward slope is gradual until the point at which the breakers curl over. But the slope is complicated by the presence of the low "outer ridge" (resulting in the holding-up of water behind it to form a moat) very near the breakers.

This ridge may perhaps be regarded as a fusion of the irregular, *Melobesia*-covered coral masses of the slope, which fill up much of the moat immediately to landward of the ridge ; the fusion of such masses reaching a maximum in the ridge itself. In this case the growth of corals towards and among the breakers is very rich. All the seaward zones are veneered by living *Melobesia* at Yonge Reef, but on other similar reefs these are less conspicuous.

It appears justifiable to compare the rocky seaward pavements of the more and less sheltered reefs of the Barrier, since they are made of similar material, and occur in each case in the same relations and at similar levels ; the differences may be correlated with the variations in their exposure to waves. The "lithothamnion ridge" described by Mayor in his account of the fringing reefs at Maer Island in the most northerly region of the Great Barrier is evidently another variety of this pavement.

When we turn to true atolls it is more difficult to be sure of our ground, because here complications are involved which are not necessarily present in the Great Barrier region. At the same time it is probably fair to compare the Oceanic margin of the rocky rim of Funafuti or of Minikoi with the Oceanic margin of Yonge Reef. However different the history of these several structures may have been, the similarity may well be due to comparable combinations of conditions. There seems to be a distinct correspondence between the rocky "reef-flat" followed to seaward by a "fissure zone" ("lithothamnion zone" of Funafuti) of these atolls, and the seaward parts of Yonge Reef, where the zone centring about the outer ridge, though less fissured than the outermost zone of the atolls, may nevertheless be the equivalent of a "fissure zone."

That these pavements, as well as the rocky reef-face which descends from them, may be superficial structures, is suggested by the borings both at Funafuti and at Low Isles ; and although these reefs are so different that no far-reaching comparison between them is possible, they may, in this particular, resemble one another. This idea is expressed for Funafuti by Sollas (Funafuti Report, p. 27), when he says : "Thus too much stress must not be laid on the unconsolidated material met with in our bore-holes ; the exterior of the atoll may be faced with solid limestone, which, like a retaining wall, may hold up the looser deposits within." In the case of Low Isles such knowledge as we possess indicates that the reef-face is rocky and that the flat is underlain by mud.

Even from this brief comparison of reefs it will have been noticed that there is no uniformity of usage with regard to the nomenclature applied by different investigators to the several parts of the reefs which they describe. Thinking that uniformity of nomenclature is desirable wherever it can be attained, we studied a number of accounts of reefs with the idea that some standard set of terms might be worked out, taking as a model, for instance, the classical report on Funafuti. The variation from one to another, however, is so great that no degree of uniformity seems to be attainable. On reflection it is proper that, at the present stage of our knowledge of reefs, this should be the case. The number of different kinds of reef in existence is considerable ; and the workers on each type have developed a nomenclature which was locally suitable. An attempt to apply the same terms throughout would involve the assumption that the several features named were homologous throughout the series ; and at present we are not in a position to establish general homologies with any degree of security. The existing nomenclature offers serious difficulty only when a single term has been employed in widely different senses ; but this can only be corrected when fuller knowledge makes a definitive classification possible.

Further comments on the reefs of the Great Barrier will be found in the next section.

SUMMARY AND CONCLUSIONS.

(By T. A. STEPHENSON.)

The following statement provides a summary of the foregoing pages, supplemented by an interpretation of the principal structural features which have been described. This aims at making it possible to view the numerous facts set out above in proper perspective, and at indicating the connection which exists between the history and structure of the reefs and the history and composition of their flora and fauna. The view of the reefs outlined here has developed from the joint ecological and geographical work of the expedition; but it makes no pretence to be anything more than a working hypothesis which correlates the facts as we know them up to the present time. Full discussions of the reefs from the geographical point of view will be found in papers recently published by J. A. Steers (1929, 1930*) and M. A. Spender (1930).

I. SEAWARD SLOPES.—The seaward slopes of all the reefs examined by us are those places in which abundant growth of living coral is taking place. This cannot fail, even if very slowly, to add substance to the reef face; since, as the coral dies, part of it, already attached to the pre-existing dead coral of the slope, will become an integral part of that slope. This must be the case, even if the greater part of the living coral were torn up in times of storm, and were deposited, some of it farther down the seaward slope and some of it on the edge of the reef. On the basis of this argument the assumption which has often been made, that the reef grows slowly outward (it cannot grow upward once it has reached the surface), appears to be perfectly reasonable.

II. ROCKY PAVEMENTS.—We have described rocky pavements or platforms of several kinds in connection with several reefs. Some of these appear to form a series. It has been argued (p. 91) that the seaward parts of Yonge Reef, the windward pavement of Batt Reef, and the windward shelf of Low Isles, are probably homologous structures. In the light of this the true importance of the windward shelf at Low Isles, at first sight so inconspicuous, becomes apparent; it is to all appearance the normal rocky reef-margin of the surf-zone; but attention is distracted from it by the more obvious structures, the ramparts, mangrove swamp and cay.

III. REEF FLATS.—We have no knowledge of the actual conditions which induce the formation of sandy reef-flats; but such flats may reasonably be regarded as accumulations of sediment which appear during certain phases of the development of reefs subject to given conditions. At Low Isles there is the complication that part of the reef-flat is rocky, consisting of the honeycomb-rock described on p. 52 and illustrated in Text-fig. 8. The explanation of the presence of this is not clear. Flat slabs of coral rock can and do arise *in situ* on reef-flats (Plate VIII, fig. 4; Plate IV, fig. 1), by the gradual lateral extension, in shallow water, of colonies of corals, such as *Porites*, which die on the top, but remain living for some time round the edges. By the fusion of such masses fairly extensive platforms may be formed, and this probably explains the origin of the rocky area in the western and middle moats, mentioned on p. 49. On the other hand, the main tract of honeycomb-rock of the Low Isles flat is so extensive and of so suggestive a shape that it seems possible that it is due to another cause. Whether it represents some earlier position of a marginal pavement, or a vestige of some other former state of the reef, is a question

* Steers' 1930 paper is report No. 1 in this volume.

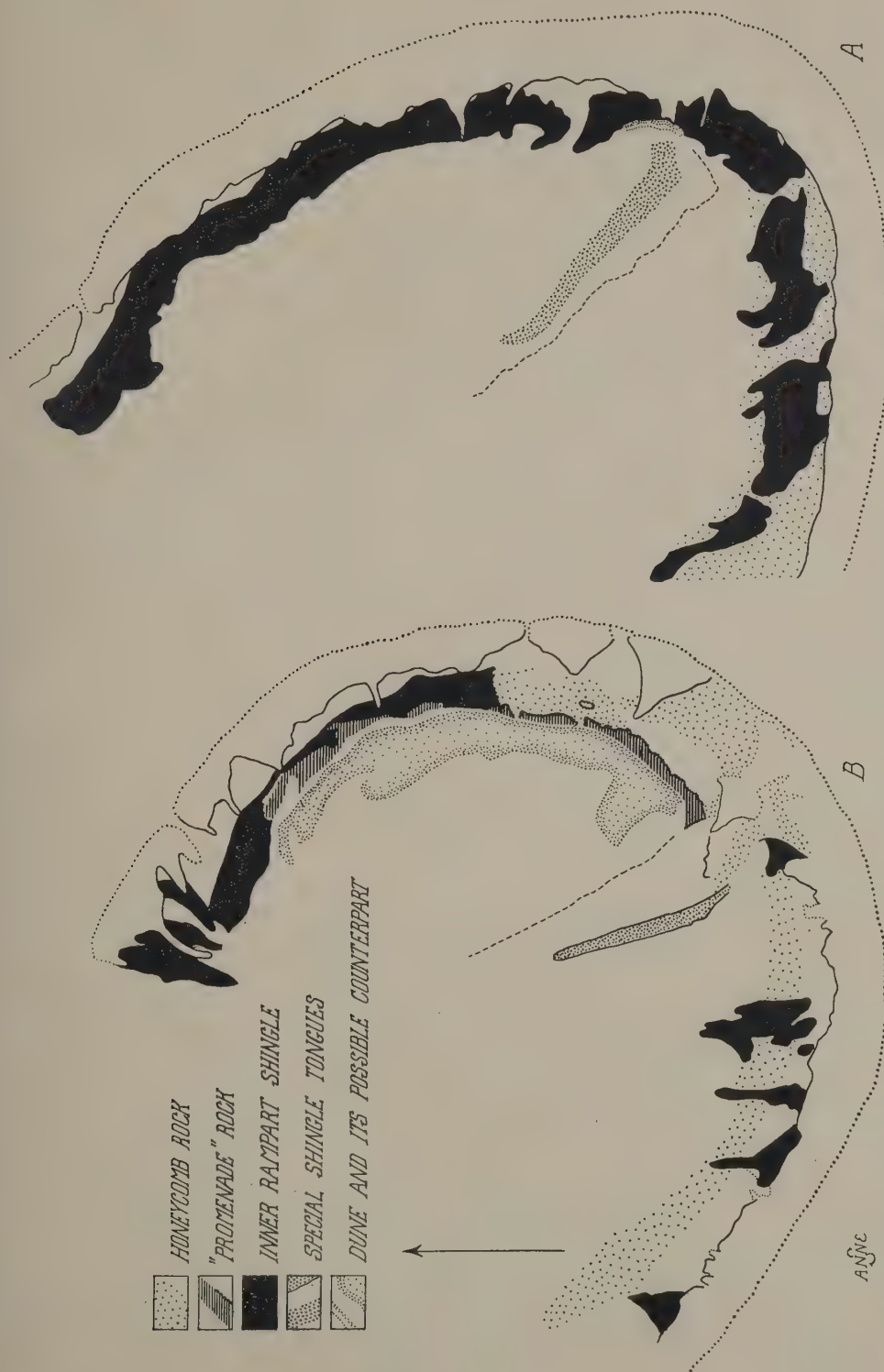
for the decision of which we have so far insufficient data ; the possible explanations which we have proposed to ourselves are open to too many objections to enable us to present any one of them with confidence. On the other hand, it may be noted that there are several agencies at work on the reef, both at and beneath the surface, which may tend towards the disintegration of coral rock on the flat. These agencies include, apart from the ordinary activities of boring organisms, bacterial liberation of CO_2 during disintegration of organic material contained in the rock itself (derived from boring and crevice-living forms), in the sand associated with it, and in the mangrove mud (see p. 70).

IV. DISPOSAL OF DEBRIS.—It may be argued that the fate of reef-debris will depend upon local conditions—upon the angle of the seaward slopes ; the level of the top of the reef ; the strength of the waves to which the reef is exposed ; the depth to which their destructive action is effective in stormy weather ; the nature of the coral growth upon the slope ; and the level at which the maximum growth of coral occurs. If this be the case the disposition of debris will vary not only on different reefs, but in different parts of the same reef, according to the exact combination of the factors concerned, at any particular spot. On a reef such as Yonge Reef there is no significant amount of debris on the oceanic side until the boulder zone is reached ; but there is, doubtless, an accumulation of it down the steep seaward slope. At Low Isles there is a great accumulation of surface debris, much of it of a comparatively fine grade, round the windward arc (ramparts), and on the seaward slope at the south-east corner there is the curious double profile, gradual at first, then steeper, and afterwards more gradual again, described on p. 64. These changes of angle possibly indicate the situation of debris which has descended the slope. On the leeward side there is the boulder tract, where large surface-debris reaches its maximum ; and this is probably to be explained as the result of the action of occasional hurricanes blowing from a direction opposite to that of the prevailing wind and tearing up large masses of coral which have become unusually unwieldy or unstable, growing into exaggerated shapes, as a result of the sheltered conditions under which they usually live.

V. RAMPARTS, MANGROVE SWAMPS AND CAYS.—Here I wish to make three points. First : That the “ island reefs ” in the steamer channel off the Queensland coast north of Trinity Opening (Class V reefs of Spender) are *coral reefs* upon which ramparts and mangrove swamps have been formed as superficial structures. The reefs upon which these structures lie have their flats at an unusually high level* (probably as the result of a slight degree of emergence which they share with the mainland), and are anomalous also in the fact that their flats, if we may judge from the borings at Low Isles, are underlain by soft mud. But the reef proper, without its superficial additions, may be regarded in the present state of our knowledge as consisting of the windward pavement and seaward slope, with their reef-flat ; and in this sense resembles an “ inner reef ” such as Batt Reef, and is, from a biological point of view, of an ordinary kind. Cays, as opposed to ramparts, can and do appear on reefs which we believe to be of lower level than those of Class V ; on a reef of the latter class the cay will antedate the rampart.

Second : The conditions which are responsible for the formation of these cays, ramparts and swamps (discussed fully by Spender, 1930), appear to be connected with the size, shape, level, orientation and situation of the reef, which factors may be held to

* The level of the flat has been ascertained by measurement only in the case of Low Isles ; but “ so far as is known this is also in agreement with the flats of the other reefs of this type.” (Spender, 1930, p. 285.)



TEXT-FIG. 15.—An attempt to compare the inner rampart of Low Isles (represented in solid black in fig. A), with the region which occupies a corresponding position at Three Isles. The areas of shingle at Three Isles which are most similar to inner rampart material at Low Isles are represented in black, and the narrow bank of shingle at Low Isles which possibly corresponds to the Three Isles dune is indicated in the same convention as the dune. For further details see p. 96. The two very long shingle-tongues shown probably do not correspond exactly—the one in fig. A lies *inside* the border of the mangrove area and probably has an exact counterpart at Three Isles (as yet unsurveyed). Similarly, the long tongue of Three Isles, which lies *outside* the border of the mangrove area, may correspond to an ill-defined ridge which occupies an almost exactly similar position in the mangrove park at Low Isles.

determine the degree and incidence of the wave action to which it is exposed. On this interpretation cays will be products of one combination of conditions, ramparts of another, but mangrove swamps are apparently a development which, under suitable circumstances, will follow the formation of ramparts. A rampart having been formed, mangrove seedlings can establish themselves on its inner scarp and on the flat in its shelter*; in time they will spread, and creating their own mud from the decay of mangrove material, they will form a swamp on the top of the sand of the flat.

Third: That ramparts appear to be able to encroach for a certain distance only over the reef-flat† and that one wave of shingle follows in due course upon another. This suggests that rampart systems probably undergo a cyclic type of development after their inception, so that the exact state of affairs on any one reef will represent a phase in the cycle. Thus the inner rampart at Low Isles is compacted and partly transformed into conglomerate and is also considerably eroded; the outer rampart is encroaching upon it and is loose and comparatively recent. At Three Isles (Text-fig. 15), there is no inner rampart proper, though a region of shingle very like one exists for a short distance; but the area between dune and outer rampart presents a complex structure and includes the promenades of hard rock described on p. 30. These two regions correspond both in shape, width, height, and relations on the two reefs; and we interpret this correspondence as meaning that the promenades at Three Isles may be the remains of a former rampart which has undergone not only a further transformation into rock than the inner rampart at Low Isles, but also a greater degree of erosion, so that the softer parts have been extensively dissected away. The honeycomb rock which figures in this area at Three Isles has the appearance of forming part of the windward platform of the reef, but it is conceivable that even this represents, in part, the planed-down vestige of former ramparts. The dune of Three Isles appears to be a structure comparable to a narrow bank of loose shingle‡ which is present along part of the inner edge of the inner rampart at Low Isles; but the dune has reached a much more highly developed condition, and has attained a size and height which enable it to support dry land vegetation.

VI. To my mind it has emerged clearly from the work of the expedition that it is at present improper to speak of "a typical coral reef," and that, if such a thing exists, it cannot yet be defined. It might be argued that the phrase "a typical coral reef" could be used in two senses—on the one hand as referring to reef-structure, and on the other as expressing the biological point of view; but in either case a deeper knowledge is needed both of the foundations of reefs, and of the biological processes which take place on them, before we can make any statement as to what, if anything, is typical. This affects the question of Low Isles in the following sense: with the reservations just made, and from the biological point of view, Low Isles may be regarded as a reef which (apart from its distinction in bearing ramparts, etc.) is as near to being a "typical" reef as many another. It must at least be defined as a coral reef.

* See Plate IV, figs. 2-4; Plate XI, fig. 2; Plate XII, fig. 4; Plate XIII, fig. 4.

† This must of course be taken as applying to reefs subject to conditions similar to those which obtain at Low Isles. Measurements of the distances which the shingle of the inner rampart has actually traversed at Low Isles, and of comparable distances at Three Isles, suggest that the limiting distance for the travel of shingle is of the order of 700 ft. from the low-water margin of the reef; it is perhaps a little greater for Three Isles than for Low Isles, because of the greater violence of the wind at the former place. The very long tongues do not appear to belong to the same system and are not included in this reckoning.

‡ This bank is shown in Plate XXVII and in Text-fig. 15, and part of it in Plate XIII, fig. 2.

VII. The content of the last paragraph may appear self-evident to anyone who has read this report ; but it has not always been realized. It has been frequently suggested verbally, and at least once in print, that Low Isles is "not a typical coral reef," from which the conclusion is sometimes drawn that it does not illustrate favourably the problems of reef formation and reef biology in general. This idea is erroneous ; the coral growth at Low Isles is, in fact, thoroughly varied and luxuriant ; but it must be sought in the proper places. Elsewhere in the Great Barrier region it is, perhaps, surpassed, as for instance in parts of Yonge Reef, but by little. Several of Saville Kent's well-known photographs of rich coral growths might easily have been secured at Low Isles, and were actually taken on a similar island reef. It must be remembered that many of Kent's photographs represent coral-associations belonging to comparatively low levels, and exposed only at extreme tides—growths which were chosen for their attractive quality from the point of view of a photographer. It is possible to walk for miles along many a reef of the Great Barrier without seeing anything of the sort, and so long as the proper zones were not sought out, a "Saville Kent" picture might never be seen at all.

VIII. THE SHAPES OF REEFS.—Low Isles is a reef of curious shape. The logical outlines for reef-systems of this type, which might be expected to result from the moulding effect of the forces to which they are exposed, include that of Three Isles (a simple ovate) and also horse-shoe forms. Low Isles presents, however, the curious embayment in its south-west coast which distorts it from a simple shape. This is perhaps due to a double foundation : Low Isles may be founded not upon one reef, but upon two or more, lying close to one another, which grew together or became united by infilling of sediment at a certain phase in their history. Several features suggest this, among them the existence of the south-west shelf (this would be the small windward shelf of the smaller and more sheltered of the two reefs) and the difference of level between the eastern and western parts of the flat.* This leads on to the observation which should be kept in mind during the future study of such reefs, that the exact form of a mangrove, rampart and cay-bearing system may be expected to depend first upon the size, shape, number and relative positions of the reef patches upon which it is founded, and upon the depths from which they grow, and later upon the effects of currents and of the waves created by the prevailing south-east wind (Text-fig. 3) ; but this second influence cannot always obliterate the effects of the first.

IX. The history of Low Isles must, therefore, be somewhat as follows. Reef patches of the type described on p. 88 at first grew up from the sea floor, bearing living coral on the top as well as down the sides. On reaching the surface the coral on top was killed, leaving only the seaward slopes to add to the substance of the reef. A windward pavement and a reef flat were formed in connection with the reaching of surface level. During the later stages first a cay and subsequently a rampart were developed, and after this a mangrove swamp. This outline, whilst omitting much, gives enough to make possible an analysis of the flora and fauna.

X. The fauna and flora of Low Isles, therefore, include the following elements :

1. The rich and varied growth of corals and alcyonaria which is proper to submerged reef patches (*cf.* the one described at Lizard Island, p. 88), but which at Low Isles has

* The general level of the eastern part of the flat is about 4 ft. above datum, this region being bounded approximately to westward by a curve running from Tripneustes Spit to M1. The western flat (*i. e.* the Sand flat and Thalamita flat) lies about $2\frac{1}{2}$ –3 ft. above datum.

survived only on the seaward slopes and in the anchorage. Associated with this growth are other organisms of various kinds, amongst which clams and fishes are conspicuous.

2. A purely secondary growth of coral, of a limited number of species, which has been able to establish itself in the pools of the flat, especially the moats; together with associated organisms.

3. A series of plants and animals which are able to stand the conditions of a tidal flat. Apart from those which bury themselves in the sand, and which are, therefore, segregated, these organisms tend to be ubiquitous on the flat; but since the flat varies in nature from place to place in a number of ways (nature of substratum, depth of pools available at low water, vicinity of mangroves, etc.), so does the fauna and flora vary subtly in composition, certain species tending to congregate most distinctly in regions where particular combinations of these conditions occur.

4. The presence of the ramparts provides a habitat found only on reefs of certain kinds, and situated at a fairly high level; with it are associated a fauna and flora of in-crusting or crevice-living forms which draw their population not only from the reef-flat series of species, but also from that of the mangrove area. It is also a special feature of the ramparts that certain animals which, on a mainland shore or on a reef with no rampart, would perforce occupy different habitats, choose the ramparts as a particular headquarters. The inner rampart is intermediate between the mangrove area and the outer rampart in population as in position.

5. The presence of the mangrove swamp introduces a new element into the fauna and flora. In the first place it carries with it a population of forms which would normally have no connection with the fauna of a reef. Secondly, it provides migrant species which escape beyond it and affect the fauna of ramparts and mangrove park. Thirdly, it provides curious areas, the mangrove park and parts of the swamp itself, in which reef conditions and woodland conditions are mixed, and in which, although a number of the reef organisms are able to flourish, the nature of the fauna and flora is recognizably modified. Certain organisms such as the hydroid *Myrionema amboinense* and the alga *Caulerpa verticillata* seem to be particularly at home under these peculiar conditions.

6. In addition to the graded series of regions just enumerated, in which the original fauna of the reef and the introduced fauna can to some extent mingle, there is dry land, which supports associations of its own sharply different from those of the rest of the reef. Dry land organisms and mangrove organisms meet in the swamp, but between those of the dry land and those of the reef there is little contact.

7. The zonation of life according to level, therefore, follows broadly the regions already indicated: from above downwards, dry land; beach sandstone and ramparts; flat and mangrove swamp; seaward slope and anchorage. On the sandstone and ramparts, however, there is further zonation from the higher to the lower parts, and the same applies to the seaward slope and anchorage, on which coral species in particular exhibit a distinct zonation. On the flat zonation is less apparent, since the factors which regulate distribution there (see paragraph 3) differentiate the region horizontally more than vertically; but even here it is the variations in level which determine the depth and extent of the pools available at low water; and they may be effective in other ways.

8. The fauna and flora of the other reefs which have been described may be understood in their relation to those of Low Isles with little further comment. Three Isles offers an almost exact parallel to Low Isles. Some of the reef-patches off Lizard Island

provide a picture of the population of reefs which are submerged or occasionally slightly exposed at low water of springs, and which possess no reef-flat. Yonge Reef has a flora and fauna of a similar nature, in which corals, alcyonaria, clams and Melobesieae are conspicuous; it is essentially the population of a submerged reef adapted to the immediate vicinity of the Pacific, but one which partly uncovers a limited number of times in the year. Batt Reef is a case in which the principal development of this typical population is restricted to the fringes, the advent of a vast sandy flat having introduced modifications of a new type, with correlated faunal and floral changes. Low Isles and Three Isles represent a still greater modification from the conditions of a submerged reef-patch. In all these cases the general level of the top of the reef is an important factor in determining the conditions which affect organisms.

A COMMENT ON THE INSTRUMENTAL SURVEY.

(By M. A. SPENDER.)

The need for a second geographical comment in these reports is not immediately apparent. The second geographer's work was survey. Nevertheless, the fact that the maps and sections resulting therefrom are published here, calls for some explanation. These detailed surveys of two reef systems were made in close collaboration with the biological side of the expedition; the interdependence of the two aspects of reef work was apparent to us in the field, and indeed it is apparent in these published reports. Some discussion of the surveys from a geographical point of view has been published elsewhere (*Geographical Journal*, vol. lxxvi, 1930, pp. 193 and 273); but the maps and sections are published here out of the necessity of the biologists. It is fair to say that hitherto the workers on coral reefs have had to manage as best they could on pre-existing maps of small scale. Although at Funafuti they had a special survey, they were handicapped in the same way in describing the detail of the reef's surface; for charts are constructed to assist mariners in steering with safety amongst reefs. Structure of the reef itself is outside the hydrographer's scope.

That there was no precedent to guide our work gave us some difficulty in the conventional representation of an amphibious region. It was necessary to evolve a set of symbols that were as far as possible self-expressive, and that could modify one into another according to the changes in the reef surface. Those embodied in this report were worked out by collaboration between the biological and the geographical parties, and are not the least important part of the work.

To my mind the most weighty constituent of our joint work was that connected with levels. On the results of this expedition, we are able to state, with a high degree of accuracy, that such a part of the reef or such a zone of corals is found at a level so many feet above or below datum or mean sea-level. The value of the accurate relation, where estimation can be so misleading, of organisms to tide levels is readily appreciated. The figures, so easily expressed, were not always simply obtained; in particular this work depends on the erection of a tide-gauge. A tide-gauge is expensive, cumbersome to transport, difficult to erect and an anxiety to maintain in running order. But without proper

reference to extreme tides and mean sea-level, the detailed biological traverses described in a subsequent paper would lose much of their value. This quantitative work will only fully assert itself when other work is available with which the Low Isles work can be compared.

It is true that if a geographer could achieve no more than a faithful record of the island reef as he saw it, his science would be amply served. If that first party of investigators, Captain Owen Stanley, J. Macgillivray and T. H. Huxley, who landed on Low Isles eighty years ago, had been able only to make it indubitably clear how many islets lay on the reef, we who followed them would have been grateful. Had the position in which they lay been charted, the whole course of the geographical work and conclusions might have been different. That of which we are sure may seem shamefully scanty to us, but on its sureness will its value to anyone else depend.

DESCRIPTION OF THE SURVEY.

LOW ISLES.

A base line was measured with a steel tape on the high eastern part of the flat; no elaborate precautions were taken. This was extended to the beacon stations (marked Δ), whose positions were fully triangulated. Tacheometric traverses were run with the theodolite between these stations outside the mangroves and along some parts of the rampart. The rest of the detail was plotted in with the plane table, except for the inside of the mangrove swamp, where the photographs made by 101 Flight of the R.A.A.F. were adjusted to show the open glades.

The soundings were made with a hand lead-line from an open boat, positions being plotted with the sextant and station pointer, and adjustments for depth taken from the recording tide-gauge.

The levelling was done with a Watts-Zeiss reversible level, most of the traverses being closed. The permissible error was 0.03 ft. per mile, such errors as occurred being due to the difficulty of finding a secure foundation for the staff.

The triangulation points were marked with stakes of stainless steel specially supplied by Messrs. Firth of Sheffield. These stakes were very convenient for this purpose and and for every other occasion where a position and level had to be left in the reef for the course of the work.

Throughout the survey, difficulty was experienced on account of the distortion of the paper in the climate.

THREE ISLES.

This was a quick survey. The base-line was measured on the flat tacheometrically while the flat was still covered by the tide. The beacon stations were intersected from the extended base-line.

A compass and tape traverse was run outside the mangroves. The remainder of the detail was filled in with the plane-table and paced compass traverses between previously fixed points. No levelling or sounding was attempted.

APPENDIX.

The types of rock mentioned in this paper come under the following headings.

A. BEACH SANDSTONE.—A rock composed of sand derived from the skeletal remains of coral and other organisms. The grains are cemented together by calcium carbonate deposited between them. This rock occurs only round the slopes of sand cays, on the reefs here described.

B. SHINGLE CONGLOMERATE.—A rock formed from coral shingle, which, on the reefs described, occurs only in connection with shingle ramparts or with regions which may represent the remains of such. It is not found among the part of the shingle which appears to be the most recent.

C. CORAL ROCK.—This phrase is employed in the present paper as a general term covering both boulders made of dead coral and more continuous masses or pavements which are also made of dead coral. It includes besides these the “promenades” of Three Isles, which, although described simply as “coral rock,” may be thought of as a derivative of shingle conglomerate.

D. HONEYCOMB-ROCK.—This is a special case of “coral rock,” and is defined on p. 52.

REFERENCES.

It seems needless to give here an extensive bibliography of works relating to coral reefs, since one has recently been published by W. M. Davis ('The Coral Reef Problem,' American Geographical Society, special publication No. 9, New York, 1928, p. 549). We therefore give a brief analysis of such of the literature as has proved most interesting and useful to us in the preparation of this report, with the aim of providing an introduction to the whole literature of the subject. Further references may be obtained from the works quoted.

1. *The Coral Reef Problem in General.*

DARWIN, CHARLES. 1842. On the Structure and Distribution of Coral Reefs, pp. xii + 214, 3 maps, text illust. London.

DAVIS, W. M. 1928. The Coral Reef Problem. American Geographical Society, special publication No. 9. New York. Pp. v, 596, 15 pls., text illust.

GARDINER, J. STANLEY. 1915. Submarine Slopes. Geogr. J. XLV, pp. 202-219, 2 pls., text illust.

2. *The Australian Barrier Reef.*—A valuable account of the Barrier Reef will be found in the work of Jukes; very fine photographs in that by Saville Kent; a useful summary of the literature in the paper by Steers; the most recent discussion of the reefs in that of Spender; and various information in the two volumes of reports of the Great Barrier Reef Committee.

FLINDERS, M. 1814. A Voyage to Terra Australis, 2 vols., illust. London.

GREAT BARRIER REEF COMMITTEE. Two volumes of papers have been published for this Committee; the first in 'Trans. Royal Geogr. Soc. Australasia' (Queensland) 1925; the second issued direct as 'Reports of the Great Barrier Reef Committee,' Brisbane, 1928.

Vol. I contains the following papers in the order here given:

RICHARDS, H. C., and HEDLEY, C. A Geological Reconnaissance in North Queensland, p. 1.

MARSHALL, P., RICHARDS, H. C., and WALKOM, A. B. Recent Emergence at Holbourne Island, Great Barrier Reef, p. 29.

HEDLEY, C. The Natural Destruction of a Coral Reef, p. 35.

HOGAN, J. Record of Sea Temperatures observed at Willis Island during the Cyclone Season of 1922-1923, p. 41.

ALEXANDER, W. B. Sea-birds of the Great Barrier Reef, p. 47.

PARADICE, W. E. J. The Pinnacle or Mushroom-shaped Coral Growths in Connection with the Reefs of the Outer Barrier, p. 52.

HEDLEY, C. A Raised Beach at the North Barnard Islands, p. 61.

— The Townsville Plain, p. 63.

— Coral Shingle as a Beach Formation, p. 66.

— An Opacity Meter, p. 67.

— A Disused River-mouth at Cairns, p. 69.

JARDINE, F. The Physiography of the Port Curtis District, p. 73.

— The Development and Significance of Benches in the Littoral of Eastern Australia, p. 111.

— The Drainage of the Atherton Tableland, p. 131.

HEDLEY, C. The Surface Temperature of Moreton Bay, p. 149.

— The Queensland Earthquake of 1918, p. 151.

Vol. II contains the following:

RICHARDS, H. C. Scientific Investigations on the Great Barrier Reef, Australia, p. vii (includes log of boring on Michaelmas Cay, p. xii, and notification of G.B.R.E.).

STANLEY, G. A. V. The Physiography of the Bowen District, etc., p. 1.

EDGEELL, J. A. Some Remarks on Coral Formations, p. 52.

— Changes at Mast Head Island, p. 57.

BRYAN, W. H. The Queensland Continental Shelf, p. 58.

JARDINE, F. The Topography of the Townsville Littoral, p. 70.

— The Broadsound Drainage in Relation to the Fitzroy River, p. 88.

— Bramble Cay, Torres Strait—Geological Notes, p. 93.

— Darnley Island—Geological and Topographical Notes, p. 101.

PARADICE, W. E. J. The Divergence of the Ends of the Great Barrier Reef from the Coast, p. 110.

The Committee has also issued the following booklet :

The Great Barrier Reef of Australia. A popular account of its general nature, compiled by the Great Barrier Reef Committee, Brisbane, 1926. Queensland Govt. Intelligence and Tourist Bureau, Brisbane. 32-page pamphlet. A new edition of this has been issued since the termination of the Expedition.

JUKES, J. BEETE. 1847. Narrative of the Surveying Voyage of H.M.S. "Fly," 2 vols. London.

KENT, W. SAVILLE. 1893. The Great Barrier Reef of Australia: Its Products and Potentialities, pp. xvii + 387, 64 pls. (col.), 1 map, text illust. London.

SPENDER, M. A. 1930. Island Reefs of the Queensland Coast. Geogr. J. LXXVI, Parts I and II, pp. 193-214; Part III, pp. 273-297; 8 pls., 2 maps; 9 text illust.

STEERS, J. A. 1929. The Queensland Coast and the Great Barrier Reefs. Geogr. J. LXXIV, Part I, pp. 232-257; Part II, pp. 341-370; 8 pls., 1 map; 8 text illust.

3. *References to Low Isles.*—These will be found in the following works. Some short articles on the fauna of Low Isles, written by members of the staff of the Australian Museum after visiting the Barrier Reef Expedition, will be found in the Australian Museum Magazine, vol. iii, 1928-9, pp. 313, 330, 366. The results of the Geographical section of the Expedition are published in the papers listed under section 2 of this list, by Steers and Spender.

KING, P. P. 1827. Narrative of a Survey of the Intertropical and Western Coasts of Australia, 2 vols. London. (Low Isles, I, p. 207.)

MACGILLIVRAY, J. 1852. Narrative of a Voyage of H.M.S. "Rattlesnake," 1846-50, 2 vols. illust. London. (Low Isles, I, p. 101, etc.)

WHARTON, W. J. L. 1893. Captain Cook's Journal during his First Voyage. Edited by Capt. W. J. L. Wharton, pp. lv + 400, 4 pls., 1 port., 7 maps. London. (Low Isles, p. 274.)

4. *The Ecology of Coral Reefs.*—The following works provide an adequate introduction to this subject:

BAKER, J. R. - 1925. A Coral Reef in the New Hebrides. Proc. Zool. Soc. London, pp. 1007-1019, text illust.

— 1929. Man and Animals in the New Hebrides, pp. xiv + 200, 17 pls., 1 map, text illust. London.

CARY, L. R. 1914. Observations upon the Growth-rate and Ecology of Gorgonians. Pap. Tortugas Lab. Wash. V, pp. 79-89, 2 pls.

— 1918. The Gorgonaceae as a Factor in the Formation of Coral Reefs. Pap. Dept. Mar. Biol. Carn. Inst. Wash. IX, pp. 341-362, 5 pls., 1 map.

CROSSLAND, C. 1928. Notes on the Ecology of the Reef-builders of Tahiti. Proc. Zool. Soc. London, pp. 717-735, 5 pls., 1 text illust.

GARDINER, J. S. 1901-6. The Fauna and Geography of the Maldivé and Laccadive Archipelagoes, 2 vols., 100 pls., text illust. Cambridge.

HEDLEY, C., and TAYLOR, T. G. 1908. Coral Reefs of the Great Barrier, Queensland: A Study of their Structure, Life-distribution and Relation to Mainland Physiography. Rep. 11th Meeting of the Aust. Assn. Adv. of Sci. 1907, pp. 397-413, 3 pls., 6 text illust. Adelaide.

MAYER, A. G. [= MAYOR]. 1918. Ecology of the Murray Island Coral Reef. Pap. Dept. Mar. Biol. Carn. Inst. Wash. IX, pp. 1-48, 17 pls., 2 maps.

MAYOR, A. G. [= MAYER]. 1924. Structure and Ecology of Samoan Reefs. Pap. Dept. Mar. Biol. Carn. Inst. Wash. XIX, pp. 1-25, 8 pls., 4 text illust.

— 1924. Growth-rate of Samoan Corals. Pap. Dept. Mar. Biol. Carn. Inst. Wash. XIX, pp. 51-72, 26 pls.

ROYAL SOCIETY, LONDON, CORAL REEF COMMITTEE. 1904. The Atoll of Funafuti, etc., pp. xiv, 428, 8 pls., 18 maps, text illust.

SETCHELL, W. A. 1924. American Samoa. Part I: Vegetation of Tutuila Island. Part II: Ethnobotany of the Samoans. Part III: Vegetation of Rose Atoll. Pap. Dept. Mar. Biol. Carn. Inst. Wash. XX, pp. vi + 275, 37 pls., text illust.

WOOD-JONES, F. 1910. Coral and Atolls, pp. xxii + 392, 27 pls., 1 map, 1 port., text illust. London.

5. *Recent Work in the Dutch East Indies*.—Important work is being done at present on the coral reefs of Batavia and elsewhere in the Dutch East Indies. An account of work already published, and further references, may be obtained from the following papers :

- UMBROVE, J. H. F. 1928. De Koraalriffen in de Baai van Batavia. Wetensch. Meded. no. 7. Dienst van den Mijnbouw in Nederlandsch.-Indie., pp. 68, 33 pls., text illust.
- 1929. De Koraalriffen der Duizend-Eilanden (Java-zee). Wetensch. Meded. no. 12. Dienst van den Mijnbouw in Nederlandsch.-Indie. Bandoeng. Pp. 47, 6 pls., text illust.
- 1930. The Influence of the Monsoons on the Geomorphology of Coral Islands. Proc. 4th Pacific Sci. Cong., Java, 1929, IIA, pp. 49–54, 4 text illust. Batavia.
- 1930. The Amount of the Maximal Lowering of Sea Level in the Pleistocene. Proc. 4th Pacific Sci. Cong., Java, 1929, IIA, pp. 105–113, 3 text illust. Batavia.
- 1930. De Koraalriffen van den Spermonde-Archipel (Zuid-Celebes). Leidsche Geol. Meded. 3, pp. 227–247, pls. 40–43.
- 1930. The End of Sluiter's Coral Reef at Krakatoa. Leidsche Geol. Meded. 3, pp. 261–264, text illust.
- VERWEY, J. 1930. Depth of Coral Reefs and Penetration of Light, with Notes on Oxygen Consumption of Corals. Proc. 4th Pacific Sci. Cong., Java, 1929, IIA, pp. 277–299, 5 text illust. Batavia.

6. *Recent Work published in America*.—Apart from the work of W. M. Davis (see section 1), much important work bearing on coral reefs has been published of recent years in America. Some of this work has already been listed under other headings. In addition reference should be made to the papers from the Department of Marine Biology of the Carnegie Institution of Washington, especially to vols. V (1914), VIII (1915), IX (1918), XIX (1924), and XXIII (1926). A selection of titles is as follows :—

Vol. V :

- DREW, G. H. On the Precipitation of Calcium Carbonate in the Sea by Marine Bacteria, etc., pp. 7–45, 2 maps, 4 text illust.
- VAUGHAN, T. W. The Building of the Marquesas and Tortugas Atolls, etc., pp. 55–67.

Vol. XIX :

- MAYOR, A. G. Causes which Produce Stable Conditions in the Depth of the Floors of Pacific Fringing Reef-flats, pp. 27–36.
- Inability of Stream-Water to Dissolve Submarine Limestones, pp. 37–49.
- Rose Atoll, American Samoa, pp. 73–79, 2 pls.
- DALY, R. A. The Geology of American Samoa, pp. 93–143, 9 pls., 2 maps.
- CHAMBERLIN, R. T. The Geological Interpretation of the Coral Reefs of Tutuila, American Samoa, pp. 145–178, 7 pls., 5 text illust.
- LIPMAN, C. B. A Critical and Experimental Study of Drew's Bacterial Hypothesis on CaCO_3 Precipitation in the Sea, pp. 179–191.
- and SHELLEY, P. E. The Chemical Composition of Lithothamnium from Various Sources, pp. 193–199.
- Studies on the Origin and Composition of the Soil of Rose Islet, pp. 201–208.
- and TAYLOR, J. K. Bacteriological Studies on Rose Islet Soils, pp. 209–217.

7. *Systematic Works on Corals*.—A good introduction to coral systematics may be gained from the following works. That by T. Wayland Vaughan includes (p. 60) a bibliography of the numerous works by this author and his collaborators.

- BERNARD, H. M. 1896–1906. Catalogue of the Madreporarian Corals in the British Museum (Natural History). II–VI: The Genera *Turbinaria*, *Astraeopora*, *Montipora*, *Anacropora*, *Goniopora*, and *Porites*. London.
- BROOK, G. 1893. Catalogue of the Madreporarian Corals in the British Museum (Natural History). I: The Genus *Madrepora*. London.
- DÖDERLEIN, L. 1902. Die Korallengattung *Fungia*. Abh. Senckenb. Naturf. Ges. Frankfurt, XXVII, pp. 1–162, pls. 1–25.
- HICKSON, S. J. 1924. An Introduction to the Study of Recent Corals. Pub. Univ. Manchr. Biol. Series, no. 4, pp. xiv + 257, 12 pls., text illust.
- HOFFMEISTER, J. E. 1925. Some Corals from American Samoa and the Fiji Islands. Pap. Dept. Mar. Biol. Carn. Inst. Wash. XXII, pp. v + 90, 23 pls., 1 map.

- MATTHAI, G. 1914. A Revision of the Recent Colonial *Astraeidae* possessing Distinct Corallites. Trans. Linn. Soc. Lond. Zool. XVII, pp. 1-140, 38 pls.
- 1926. Colony-formation in *Astraeid* Corals. Philos. Trans. ser. B, CCXIV, pp. 313-367, pls. 24-28, 27 text illust.
- 1928. A Monograph of the Recent Meandroid *Astraeidae*. Catalogue of the Madreporarian Corals in the British Museum (Natural History), VII, London.
- VAUGHAN, T. W. 1918. Some Shoal-water Corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island. Pap. Dept. Mar. Biol. Carn. Inst. Wash. IX, pp. 49-234, 74 pls.

8. *Other References*.—Some miscellaneous references to papers which have been useful to us are as follows :

- BROOKS, M. M. 1929. Studies on the Permeability of Living Cells, X. Protoplasma, Leipzig. VII, pp. 46-61, 3 text illust.
- 1930. Studies on the Permeability of Living Cells, XI. Univ. Calif. Pub. Zool. XXXIII, Berkeley, pp. 287-290, 1 text illust.
- 1930. Studies on Permeability of Living Cells, XII. Proc. Soc. Exp. Biol. N.Y. XXVII, p. 508.
- BROOKS, S. C. 1929. Accumulation of Potassium in Living Cells—a Non-Equilibrium Condition. Proc. Soc. Exp. Biol. N.Y. XXVII, p. 75.
- 1929. The Accumulation of Ions in Living Cells—a Non-Equilibrium Condition. Protoplasma, VIII. Leipzig. Pp. 389-412, 5 text illust.
- 1930. Composition of the Cell Sap of *Halicystis ovalis* (Lyng.) Areschoug. Proc. Soc. Exp. Biol. N.Y. XXVII, p. 409.
- CLARK, H. LYMAN. 1915. The Comatulids of Torres Strait, with Special Reference to their Habits and Reactions. Pap. Dept. Mar. Biol. Carn. Inst. Wash. VIII, pp. 97-125.
- 1921. The Echinoderm Fauna of Torres Strait. Pap. Dept. Mar. Biol. Carn. Inst. Wash. X, pp. viii + 223, 38 pls., 1 map.
- HEDLEY, C. 1915. An Ecological Sketch of the Sydney Beaches. J. Roy. Soc. N.S.W. XLIX, Presidential Address, May 5th, pp. 15-77, pls. i-vii, text illust.
- 1921. A Revision of the Australian *Tridacna*. Rec. Aust. Mus. XIII, pp. 163-172, 8 pls., 1 text illust.
- KEMP, S. 1915. Fauna of the Chilka Lake: Crustacea Decapoda. Mem. Ind. Mus. V, pp. 199-325, 2 pls., text illust.
- MUSGRAVE, A. 1929. The Lure of a Mangrove Swamp. Aust. Mus. Mag. III, pp. 318-324, 9 text illust.
- 1929. Life in a Mangrove Swamp. Aust. Mus. Mag. III, pp. 341-347, 8 text illust.
- POTTS, F. A. 1915. *Hapalocarcinus*, the Gall-forming Crab, with Some Notes on the Related Genus *Cryptochirus*. Pap. Dept. Mar. Biol. Carn. Inst. Wash. VIII, pp. 33-69, 3 pls., 19 text illust.
- 1915. The Fauna Associated with the Crinoids of a Tropical Coral Reef; with Especial Reference to its Colour Variations. Pap. Dept. Mar. Biol. Carn. Inst. Wash. VIII, pp. 71-96, 1 pl., 7 text illust.
- PRASHAD, B. 1925. Respiration of Gastropod Molluscs. Proc. 12th Indian Sci. Cong. Presidential Address, Zool. Section, issued July, pp. 126-143, text illust.
- RISBEC, J. 1930. Étude d'un mollusque nacrier, le Troque (*Trochus niloticus* L.). Faune des Colonies Françaises, Paris, IV, fasc. 2, pp. 149-189, text illust.
- SKEATS, E. W. 1918. The Coral Reef Problem and the Evidence of the Funafuti Borings. Amer. J. Sci. (ser. 4), XLV, pp. 81-90.
- 1918. The Formation of Dolomite and its Bearing on the Coral Reef Problem. Amer. J. Sci. (ser. 4), XLV, pp. 185-200.
- WARD, M. 1927-29. The Habits of Our Common Shore Crabs. Aust. Mus. Mag. III, pp. 242-247, 5 text illust.
- YONGE, C. M. 1928. Feeding Mechanisms in the Invertebrates. Biol. Reviews, Cambridge, III, pp. 21-76, 25 text illust.

SYSTEMATIC INDEX.

ANIMALS.

PROTOZOA.		PAGE
Ciliates		70
Flagellates		70
Foraminifera		44, 70
Orbitolites complanata	44, 48, 50, 70, 90	
Protozoa		70
PORIFERA.		
Chalina camerata		38, 54
„ clathrata		38, 54
Chondrilla nucula		54
Cinachya australiensis	44, 52, 53	
Cladochalina pulvinatus		38
Clathria aculeata		44
Desmacidon reptans		54
Euspongia		90
„ irregularis var. pertusa	44, 52, 71	
Gellius fibulatus	44, 48, 49, 54	
„ pumilus		38
„ sagittarius		44, 48
„ toxius		38, 39
Iotrochota purpurea		54
Laxosuberites proteus		54
Ophlitaspongia rimosa		54
Phyllospongia foliascens	71, 86, 89	
„ ridleyi	83, 84, 86	
Polymastia		54
Porifera		44, 54, 86
Pseudosuberites andrewsi		54
Rhaphidophilus coralliophilus		54
Spirastrella aurivillii		54
„ purpurea	38, 44, 52, 71	
„ semilunaris		54
Spongelia digitata		38
Sponges	38, 39, 42, 54, 70, 71, 83, 84	
Stelletta purpurea		86
COELENTERATA.		
Coelenterata		38, 54, 59, 71
HYDROZOA.		
Aglaophenia cupressina	71, 83, 84, 86, 88	
Dynamena crisioides	44, 54, 59, 71	
Hydroids		42
Hydrozoa	44, 67, 71, 86, 88	
Lytocarpus phoenicius		67
Millepora	38, 67, 71, 86	
Myrionema amboinense	38, 44, 49, 52, 71, 98	
Sertularia		84, 86
SCYPHOZOA.		
Cassiopea andromeda		50, 71
COELENTERATA—cont.		PAGE
ANTHOZOA.		
Anthozoa		56, 71
(1) <i>ALCYONARIA</i> .		
Alcyonaria	49, 61, 64-67, 70-72, 83, 84, 86-88, 97, 99	
Alcyonium		67
Cespitularia multipinnata		67, 82
Clavularia		67
Dendronephthya		67
Gorgonians		71
Helipora	50, 67, 71, 72, 81, 86	
Heteroxenia		67
Isis hippuris		82, 88
Juncella		67, 71
Lithophytum		67
„ arboreum		86
„ digitatum		86
Lobophytum	67, 86, 87, 88	
Melitodes		67, 71
Pachyclavularia		67
Sarcophytum	64, 67, 86-88	
Sinularia	64, 67, 86-88	
„ flexibile		87, 88
Tubipora	71, 84, 86, 89	
Xenia		67, 86
„ umbellata		89, 90
(ii) <i>CERIANTHARIA</i> .		
Arachnanthus		56, 72
(iii) <i>ANTIPATHARIA</i> .		
Eucirripathes		67, 72
(iv) <i>ZOANTHINARIA</i> .		
Palythoa	65, 67, 72, 84, 86, 88	
Zoanthids	38, 49, 52, 84	
Zoanthinaria	44, 67, 72, 86, 88	
(v) <i>ACTINIARIA</i> .		
Actinaria		44, 72
Actinodendron plumosum	44, 47, 50, 54, 55	
Anemones	36, 42, 47, 58	
Anemonia citrina		57
Anthopleura		36, 59
Calliactis miriam		72
Commensals	47, 72, 73	
Cryptodendron adhaesivum		47
Edwardsia		56
Gyrostoma ramsayi		72, 87
Phellia		59
Phyllodiscus cinctus		38
Phymanthus		54, 56
Stoichactis		73, 89

COELENTERATA—*cont.*ANTHOZOA—*cont.*

PAGE

(v) *ACTINIARIA*—*cont.*

Stoichactis kenti	38, 44, 47, 49, 50, 54, 72
Thalassianthus	73
" hemprichii	47
" hypnoides	47

(vi) *MADREPORARIA*.

Acanthastrea	47
Acropora	38, 57, 62, 67, 82-86, 88, 89, 90
" brueggemanni	82
" decipiens	83, 90
" delicatula	83
" gemmafera	83, 84
" hebes	44, 46, 47, 62, 82, 84
" hyacinthus	83
" palifera	83, 85, 88
" pulchra	62, 82, 84
" squamosa	84

Actinotryx	47
Astraeids	38, 90
Astreopora	67, 86
Coeloria	67, 86, 88, 90
Commensals	47, 66, 73
Corals	26, 28, 34, 37, 42, 47, 49, 50, 53, 57, 60-62, 64-66, 70, 72, 73, 83-85, 87-99

Cyphastrea	39, 50, 54, 67, 86
Dendrophyllia	67
Diploastrea	67
" heliopora	88
Discosomidae	88
Echinopora	67, 86, 87
Euphyllia	67, 73, 86
Favia	44, 47, 54, 67, 71, 74, 80, 84, 86, 88, 90

Favites	47
Fungia	49, 67, 73, 88
Galaxea	44, 67, 86, 87, 90
Goniastrea	47
Goniopora	67, 86, 89, 90
Herpetolitha	67, 88
Hydnophora	67, 86
Leptastrea	39, 44, 50, 67
Lobophyllia	67, 86, 88
Madreporaria	44, 67, 72, 86, 88
Merulina	67, 88
Montipora	38, 64, 67, 86, 88
" ramosa	44, 46, 47, 62, 82
Orbicella	67
Oulophyllia	67, 87
Pachyseris	67, 87
Pavona	67, 81, 86, 87, 90
Platygyra	67, 86, 88
Pocillopora	67, 86, 88, 90
" bulbosa	38, 44, 47, 50, 89
Polyphyllia	67, 88

COELENTERATA—*cont.*ANTHOZOA—*cont.*

PAGE

(vi) *MADREPORARIA*—*cont.*

Porites	38, 39, 44, 46-48, 50, 54, 67, 72, 80, 82, 86, 87, 89, 90, 93
Psammocora	49, 67, 87
Rhodactis	47
Seriatopora	67, 86, 88
Stylophora	67, 86, 88
Symphyllia	67, 74, 80, 86, 88, 90
Tridacophyllia	67, 87
Turbinaria	67, 88

CTENOPHORA.

Coeloplana	72
----------------------	----

TURBELLARIA.

Turbellaria	72
-----------------------	----

NEMERTINEA.

Baseodiscus	56
" delineatus	72
" quinquelineatus	56, 72
Lineus	56, 72

ANNULATA.

POLYCHAETA.

Eurythoe complanata	44, 56, 72
Galeolaria caespitosa	70
Iphione muricata	44, 54, 72
Marphysa mossambica	56
Mesochaetopterus minuta	56
Odontosyllis hyalina	73
Perinereis obfuscata	72, 73
Phyllodoce malmgreni	56
Platynereis polyscalma	72
Polychaeta	38, 44, 54, 56, 67, 72, 86, 90
Scolecopsis indica	56
Spirobranchus	85
" giganteus	44, 48, 67, 72, 83, 86
Worms	55

OLIGOCHAETA.

Earthworms	40, 41
Pontodrilus bermudensis	40, 42, 73

GEPHYREA.

Aspidosiphon cumingii	56, 59, 60
Cloeosiphon	59, 60
Gephyrea	56, 60, 73
Physcosoma	59, 60
Sipunculoidea	37, 44, 59, 60, 73

ARTHROPODA.

CRUSTACEA.

Crustacea	47, 56, 67, 70, 73
---------------------	--------------------

(i) *CIRRIPEDIA*.

Acorn barnacles	37, 44, 54, 59, 70, 73
Cirripedia	44, 59, 73
Lepas anatifera	73

ARTHROPODA—cont.

CRUSTACEA—cont.

PAGE

(i) *CIRRIPEDIA*—cont.

Lithotrya	73
Ship's barnacles	73
Tetraclita	73

(ii) *ISOPODA*.

Cymodoce	73
Isopoda	40-42, 57-59, 61-73
Ligia australiensis	40, 42, 59, 61, 73

(iii) *AMPHIPODA*.

Amphipoda	59, 73
Ampithoe	73
Ceradocus	73
Hyale	59, 73
Maera	73

(iv) *DECAPODA*.

Decapoda	56, 73
--------------------	--------

A. *NATANTIA*.

Crangon strenuus	44, 73
„ ventrosus	44, 73
Commensals	47, 72, 73
Natantia	44, 73
Periclimenes	47
„ brevicarpalis	47, 73
„ spiniferus	47
Prawns	38, 47, 70, 73

B. *REPTANTIA*.(a) *PALINURA*.

Panulirus versicolor	67, 73
--------------------------------	--------

(b) *ANOMURA*.

Anomura	42, 44, 59, 61, 73
Callianassa australiensis	56
Callianidea	56
Clibanarius	73
„ striolatus	38, 40-42, 52
„ virescens	37, 44, 59, 61
Commensals	72
Dardanus megistos	44
Hermit crabs	38, 39, 58, 72, 73, 83, 84
Petrolisthes lamarcki	59, 61, 73
Thalassina	41
„ anomala	40, 42

(c) *BRACHYURA*.

Actaea hirsutimana	44
„ polyacantha	47
„ tomentosa	59, 86
Atergatis ocyroe	44, 47, 54, 59
Brachyura	42, 44, 54, 59, 61, 74, 86
Calappa hepatica	44, 52
Charybdis orientalis	86
Chlorodopsis melanocheirus	59
Commensals	47

ARTHROPODA—cont.

CRUSTACEA—cont.

PAGE

(iv) *DECAPODA*—cont.B. *REPTANTIA*—cont.(c) *BRACHYURA*—cont.

Crabs	38, 40, 41, 47, 57, 58, 61, 70, 74
Cryptochirus	74
Cymo andreossyi	47
Eriphia sebana	47
Euplax tridentatus	42
Gelasimus	42
„ annulipes	42
„ dussumieri	41, 42
„ tetragonon	53, 61
Grapsus strigosus	37, 82
Leptodius exaratus	59, 61
„ nudipes	59
Macrophthalmus telescopicus	56
Metopograpsus messor	42, 59, 61
Ocypode ceratophthalma	35
„ cordimana	35
Perceon abbreviatus	86
Phymodius unguulatus	44, 59
Pilumnus spinicarpus	47
„ vespertilio	44, 50, 53, 54
Scylla	41
„ serrata	40, 42, 61
Sesarma bidens	42, 61
„ villosa	42, 61
Spider-crabs	84
Thalamita admete	44, 59
„ crenata	38, 42, 52
„ stimpsoni	44, 54
Trapezia cymodoce	47
„ ferruginea	86
Zozymus aeneus	86

(v) *STOMATOPODA*.

Gonodactylus chiragra	44, 59, 74
Lysiosquilla maculata	56, 74
Squilla	84
Stomatopoda	44, 56, 59, 74

ARACHNIDA.

Arachnida	36, 74
Desis crosslandi	74
Isometrus maculatus	36
Scorpions	36
Spiders	36, 74

INSECTA.

Ants	36, 40, 41, 57, 61
Beetles	36
Butterflies	36
Cockroaches	36
Danaiida melissa subsp. hamata	36
Flies	36, 40
Grasshoppers	36

ARTHROPODA—*cont.*

INSECTA— <i>cont.</i>	PAGE
Insecta	42, 61
Mosquitoes	36, 42
Moths	36
Musca domestica	36
Oecophylla smaragdina subsp. virescens	40-42
Pheidole variabilis	36
Polyrhachis sokolova	40, 42
Sandflies	36, 40, 42
Troides priamus subsp. euphorion	41
Valanga irregularis	36

MOLLUSCA.

Mollusca	37, 56, 58, 67, 70, 74, 80, 89
--------------------	--------------------------------

AMPHINEURA.

Acanthozostera gemmata	37, 44, 53, 61, 74
Amphineura	44, 59, 61, 74
Chiton	38
Schizochiton incisus	44, 59

GASTROPODA.

Aplysia	74, 90
Baler-shell	74
Bembicium melanostoma	42, 61
Cerithium patulum	42
Clava vertagus	56, 86
Conus	74
" lividus	86
" marmoreus	86
" striatus	86
" vexillum	86
Cypraea	74
" annulus	44, 50, 59
" erroneus	44, 59
" lynx	86
" moneta	44, 86
" tigris	81
Dolabella scapula	74
Drupa cornus	86
" marginalba	59
" ricinus	86
" rubus-caesius	86
" tuberculata	59
Euthyneura	74
Gastropoda	36, 40, 41, 42, 44, 55-59, 61, 74, 83, 84, 86
Haliotis	74
Latirus smaragdulus	86
Limpets	37, 54
Melampus adamsianus	42
" granifer	42
Melarhaphe	38, 39, 52
" coccinea	80
" scabra	42, 61
" undulata	42, 61, 80
Melo diadema	44, 74

MOLLUSCA—*cont.*

GASTROPODA— <i>cont.</i>	PAGE
Nassarius coronatus	56
Natica	38, 40
" gualteriana	56
Naticidae	42, 56
Nerita	58
" albicilla	59, 61, 80
" chamaeleon	59, 80
" costata	82
" lineata	42
" planospira	42
" plicata	42, 59, 61, 80, 82
" polita	59, 80
" striata	42, 59, 61
Nudibranchs	74, 90
Onchidium	44, 50, 53, 59, 74
Ovula	74
Planaxis sulcatus	37, 59, 61, 80
Pterocera	86
" crocata	44, 52
Pyrasus	38, 40, 41
" palustris	39, 42
Pythia nux	42
Quoyia decollata	42, 61
Siphonaria	54, 80
" denticulata	44, 55, 59
Snails	38
Strombus gibberulus	56
" luhuanus	44, 56
Tectarius malaccanus	61, 80
Telescopium	38, 40, 41
" telescopium	39, 42
Terebra	74
" affinis	74
" muscaria	56
Thais armigera	86
Trochus	86
" fenestratus	44, 55
" niloticus	44, 59, 67
Turbo nivosus	59
" petholatus	59
" porphyrites	59, 61
Uber	38
" flemingianum	56
" mammilla	56
Vermetidae	37, 44
Whelks	39, 41

LAMELLIBRANCHIA

Arca fusca	45, 55, 59
" imbricata	59
Bivalves	38
Boring lamellibranchs	37, 60, 74
Cardium oxygonum	56
Chama	54
" jukesii	37, 45, 53, 55
Clams	38, 47, 62, 64, 83-85, 88, 98, 99

MOLLUSCA—*cont.*LAMELLIBRANCHIA—*cont.*

	PAGE
Cockles	38
Corbis fimbriata	56
Cyrena coaxans	40, 42
Davila plana	35
Gafrarium pectinatum	38, 42
„ tumidum	38, 42
Gastrochaena	60, 74
„ gigantea	59
Hippopus	56, 74, 85
„ hippopus	39, 45, 48, 49, 54, 55, 86
Isognoma isognomum	45
Lamellibranchs	35, 36, 42, 45, 55, 56, 58, 59, 74, 86
Lima tenera	45, 55, 75
Lithophaga	45, 60, 74
„ argentea	59
„ cumingiana	59
„ obesa	59
„ subula	59
„ teres	59
Loripes edentulus	56
Mactra maculata	56
Melina nucleus	59
Modiolus auriculatus	45, 53, 59
„ cinnamomeus	60
Mussels	70
Ostrea cerata	45
„ crista-galli	45
„ mordax	36, 40, 42, 45, 52, 59, 60, 70
Oysters	36, 37, 39, 84
Petricola lapicida	60
Pinctada margaritifera	45, 55, 67
Pinna vexillum	52
Spondylus	54
„ ducalis	45, 53, 55
Tellina palatam	42
„ remies	42
„ virgata	56
Teredo	38, 39, 42
Tridacna	74
„ crocea	39, 45, 47, 59, 60, 67, 74, 85, 86, 89
„ derasa	47, 67, 85, 86, 88, 89
„ elongata	85, 86, 88, 89
„ fossor	39, 45, 47, 48, 67, 85, 86, 89, 90
„ squamosa	48

CEPHALOPODA.

Cephalopoda	74
Nautilus	74
Octopods	74
Sepioteuthis	74
Spirula	74
Squids	74

ECHINODERMATA.

Echinodermata 55, 56, 58, 59, 67, 70, 75, 79, 86, 89

ECHINODERMATA—*cont.*

ASTEROIDEA.

	PAGE
Archaster typicus	56, 75
Asterina exigua	58, 59, 75
Asteroidea	45, 75
Asterope carinifera	77
Culcita novae-guineae	45, 75
Echinaster luzonicus	77
Iconaster longimanus	77
Linckia guildingii	84-86
„ laevigata	45, 48, 67, 75, 84-86, 89
Nardoa pauciforis	45, 75, 86
Oreaster nodosus	77

ECHINOIDEA.

Centrechinus setosus	45, 48, 75
Diadema ; see Centrechinus	
Echinoidea	45, 75
Echinometra mathaei	45, 47, 58, 59, 75, 83, 85, 86, 89, 90
Echinostrephus molare	67, 83, 86
Laganum depressum	56
Tripneustes gratilla	45, 75

CRINOIDEA.

Comatulids	76
Crinoidea	67, 75, 85, 86, 89
Lamprometra gyges	67

HOLOTHUROIDEA.

Holothuria arenicola	56
„ argus	39, 52
„ atra	45, 50, 53, 55
„ coluber	45, 48, 55
„ erinaceus	59
„ impatiens	55
„ leucospilota	39, 45, 48, 50, 55, 59, 76
„ marmorata	77
„ pardalis	59
„ scabra	38
Holothurians	38, 42, 50, 58, 59, 62, 76, 84, 86
Holothuroidea	45, 76
Polycheira rufescens	59
Stichopus chloronotus	45, 48, 67, 84, 86, 87
„ horrens	55
Synapta maculata	39, 45, 52

OPHIUROIDEA.

Ophiactis savignyi	* 77
Ophiarachnella gorgonia	77
Ophiarthrum elegans	45
„ pictum	77
Ophiocoma brevipes var. variegata	77
„ scolopendrina	45, 49, 53, 59, 75
Ophiolepis superba	77
Ophiothrix longipeda	45, 55, 75
Ophiuroidea	45, 75

POLYZOA.	PAGE
Polyzoa	76
Retepora graeffei	76

BRACHIOPODA.	PAGE
Brachiopoda	76
Lingula	76

ASCIDIACEA.	PAGE
Asciidiacea	45, 55, 59, 76, 86
Ascidians	39, 42
Botryllus magnicoecus	86
Chorizocarpa sydneyensis	84, 86
Compound Ascidians	38, 39, 76, 83, 84
Didemnum	39
„ candidum	45, 55, 59, 76
„ psammotodes var. skeati	55, 76
Diplosoma virens	39, 45, 48, 76, 89, 90
Simple Ascidians	76

ENTEROPNEUSTA.	PAGE
Balanoglossus carnosus	56
Enteropneusta	56, 76
Ptychodera flava	56

PISCES.	PAGE
Actinicola percula	47
Amphiprion bicinctus	47
Chiloscyllium ocellatum	77

PISCES—cont.	PAGE
Commensals	47, 66, 72
Fishes	38, 47, 66, 70, 77, 85, 89, 98
Himantura granulata	77
Periophthalmus	41
„ koelreuteri var. argentil- neatus	40, 42
Pisces	42
Pranesus ogilbyi	77
Pseudomugil signifer	77
Rays	77, 89
Scomberomorus commerson	77
Sharks	77
Synanceja horrida	77
Taeniura lymma halgani	77
Tetrodon hispidus	77
Zenarchopterus dispar	39

REPTILIA.	PAGE
Geckos	40-42, 77
Sea-snakes	77

AVES.	PAGE
Birds	77
Cuncuma leucogaster	77
Demiegretta sacra	77
Hérons	77
Myristicivora bicolor subsp. spilorrhoea	77
Pigeons	77
Sea Eagles	77

PLANTS.

BACTERIA.	PAGE
Bacteria	71

CRYPTOGAMS.	PAGE
ALGAE.	
Algae	48, 54, 58, 62, 64-66, 70, 84-86, 89-91
(i) PROTOPHYTA.	
Zooxanthellae	70
(ii) DIATOMACEAE.	
Diatoms	52, 70
(iii) CYANOPHYCEAE.	
Blue-green algae, 36 ; see also Cyanophyceae.	
Cyanophyceae	38, 40, 42, 45, 52, 55, 68, 69, 82, 90
Hormothamnium solutum	45, 55
Lyngbya majuscula	45, 55, 64
Trichodesmium	46
(iv) FLORIDEAE.	
Acanthophora spicifera	45, 48
Amphiroa fragilissima	45, 49, 68, 89, 90

CRYPTOGAMS—cont.	PAGE
ALGAE—cont.	
(iv) FLORIDEAE—cont.	
Digenia simplex	45, 48, 68
Florideae	45, 68
Galaxaura	49, 68, 90
Laurencia	50, 53, 54, 90
„ botryoides	45, 48, 68
„ papillosa	45, 48, 68
Lithothamnion, 46, 92 ; see also Melobesieae and Nullipores.	
Melobesieae	45, 46, 68, 69, 84, 86, 90, 92, 99
Nullipores	46, 47, 54, 57, 58, 69, 83-85, 91
Polysiphonia	48, 55
Red algae, 48 ; see also Florideae.	
Spyridia filamentosa	45, 54, 55
Squamariaceae	54
(v) PHAEOPHYCEAE.	
Brown algae, 48 ; see also Phaeophyceae.	
Cystophora	69
Cystophyllum	46, 55, 69

CRYPTOGAMS—*cont.*

ALGAE— <i>cont.</i>	PAGE
(v) <i>PHAEOPHYCEAE</i> — <i>cont.</i>	
<i>Cystophyllum muricatum</i>	45, 52
<i>Dictyota Bartayresiana</i>	45, 68
" <i>ciliata</i>	45, 68
<i>Ecklonia</i>	69
<i>Ectocarpus</i>	48, 52
<i>Hydroclathrus</i>	54
" <i>clathratus</i>	45, 49
<i>Laminaria</i>	69
<i>Padina</i>	69
" <i>australis</i>	45, 48, 68
" <i>Commersonii</i>	45, 48, 68
<i>Phaeophyceae</i>	45, 68
<i>Sargassum</i>	46, 52, 55, 65, 69
" <i>cristaeifolium</i>	65, 68
" <i>lanceolatum</i>	45, 52
" <i>latifolium</i>	45
" <i>tarvum</i>	45
<i>Turbinaria</i>	69
" <i>ornata</i>	48, 65, 68, 89, 90
" <i>turbinata</i>	45, 48, 52
(vi) <i>CHLOROPHYCEAE</i> .	
<i>Anadyomene</i>	54
<i>Avrainvillea erecta</i>	55
<i>Boodlea</i>	49, 53, 54
" <i>paradoxa</i>	45, 48, 68
<i>Bornetella</i>	90
" <i>nitida</i>	45, 68
<i>Caulerpa</i>	48, 50, 84–86, 89, 90
" <i>peltata</i>	45
" <i>racemosa</i>	45, 52, 55, 58, 68
" <i>verticillata</i>	38, 39, 42, 52, 98
<i>Chlorodesmis</i>	85
" <i>comosa</i>	65, 68, 84, 86
<i>Chlorophyceae</i>	45, 68
<i>Dictyosphaeria</i>	48, 50, 53, 54, 70, 90
" <i>favulosa</i>	45, 68
" <i>sericea</i>	45, 68
" <i>Versluysii</i>	45, 68
<i>Enteromorpha</i>	36, 69
Filamentous algae	48
Green algae ; see <i>Chlorophyceae</i> .	
<i>Halicystis</i>	70
<i>Halimeda</i>	39, 50, 84–86, 90, 91
" <i>cuneata</i>	45, 48, 68
" <i>opuntia</i>	45, 48, 52, 68
" <i>Tuna</i>	68
<i>Valonia</i>	70
" <i>aegagropila</i>	52
" <i>Forbesii</i>	48
" <i>macrophysa</i>	70
<i>Valoniaceae</i>	70

CRYPTOGAMS—*cont.*

LICHENES.	PAGE
Lichens	38, 42
FUNGI.	
Fungi	38, 42

PHANEROGAMS.

<i>Achyranthes aspera</i>	41, 42
<i>Aegialitis annylata</i>	60
<i>Avicennia</i>	82, 57
" <i>officinalis</i>	42, 57, 60
<i>Bruguiera Rheedii</i>	40, 42
<i>Cassytha filiformis</i>	35
<i>Casuarina</i>	80
" <i>equisetifolia</i>	35
<i>Ceriops tagal</i>	42
<i>Cocos</i>	80
" <i>nucifera</i>	35
<i>Commelina cyanea</i>	41, 42
<i>Cymodocea</i>	89
<i>Diplanthera uninervis</i>	49
<i>Euphorbia eremorphila</i>	35
<i>Excoecaria agallocha</i>	41, 42
<i>Flagellaria indica</i>	41, 42
Flowering plants ; see <i>Phanerogams</i> .	
Grass	82
<i>Halophila</i>	54, 55
" <i>ovalis</i>	45, 52
<i>Ipomoea pes-caprae</i>	35
<i>Jasminum simplicifolium</i>	35
<i>Josephinia grandiflora</i>	80
<i>Lepturus repens</i>	41, 42
Mangroves, 24, 25, 27, 37–42, 50, 52, 60, 82, 96, 98 ; see also <i>Avicennia</i> , <i>Bruguiera</i> , <i>Excoecaria</i> , <i>Rhizophara</i> .	
<i>Osbornia octodonta</i>	82
<i>Pandanus</i>	80, 82
<i>Passiflora foetida</i>	35
<i>Pemphis acidula</i>	82
<i>Phanerogams</i>	42, 45
<i>Premna obtusifolia</i>	36
<i>Rhizophora</i> 28, 37, 41, 48, 53, 82 ; see also Mangroves.	
" <i>mucronata</i> 24, 25, 38, 42, 45, 50, 60	
<i>Scaevola Koenigii</i>	35
<i>Sesuvium</i>	41, 81, 82
" <i>Portulacastrum</i>	40, 42, 60
<i>Terminalia</i>	80
" <i>catappa</i>	35
<i>Thalassia</i>	38, 39, 52, 54, 55, 81, 89
" <i>Hemprichii</i>	25, 45, 48, 50
<i>Thespesia populnea</i>	41, 42
<i>Tournefortia argentea</i>	36
<i>Vigna marina</i>	35
<i>Vitex trifolia</i>	36

DESCRIPTION OF PLATE I.

Chart of Low Isles.

Plates I and II reprinted, with some minor corrections, from the 'Geographical Journal,' vol. lxxvi, 1930, by permission of the Royal Geographical Society.

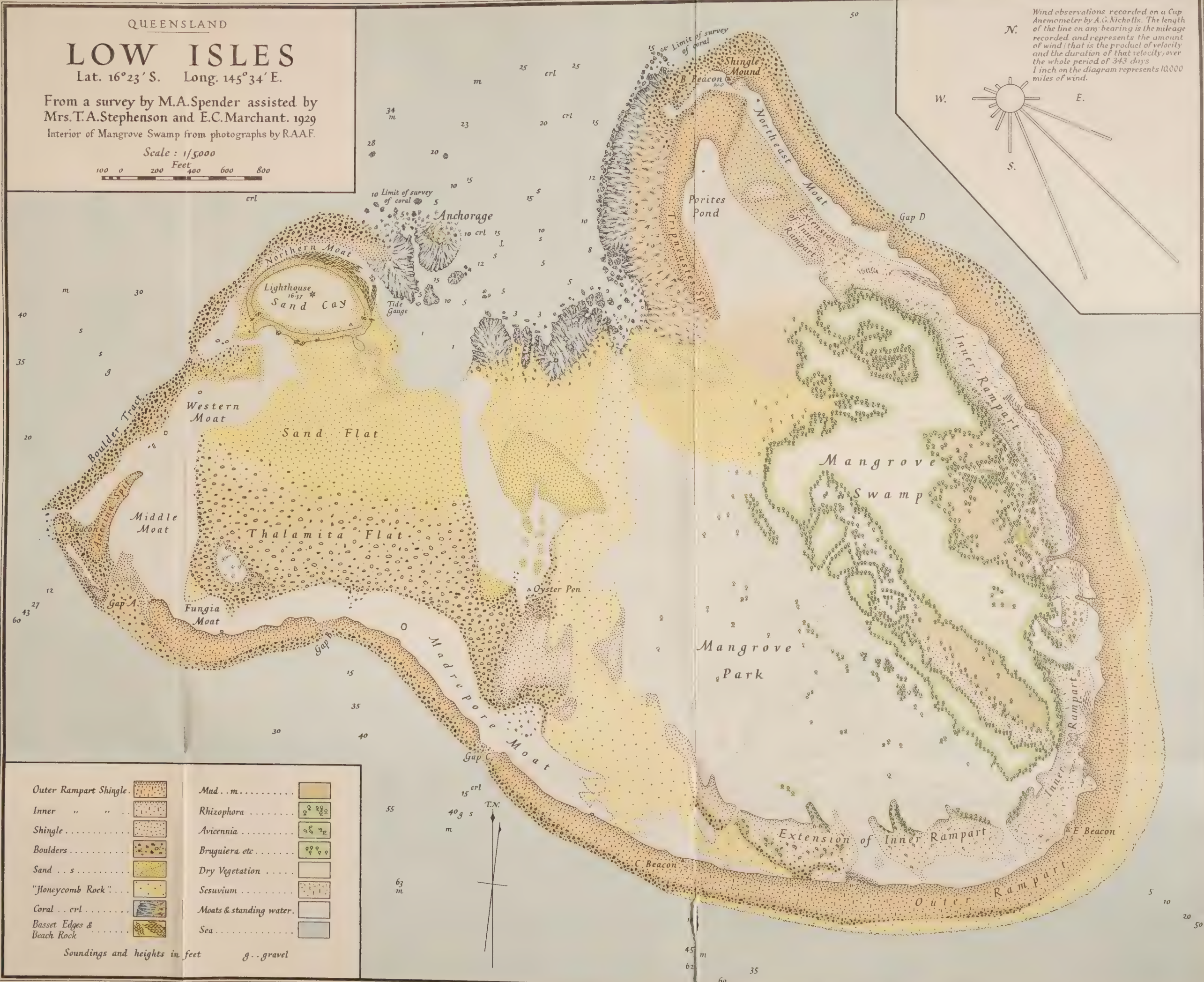
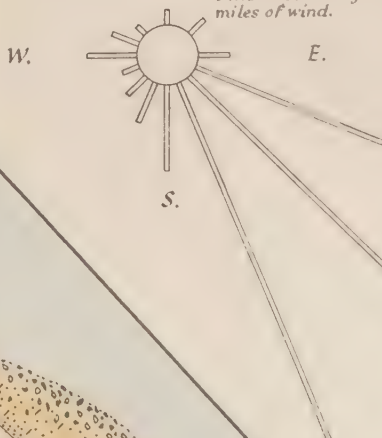
QUEENSLAND
LOW ISLES

Lat. 16°23' S. Long. 145°34' E.

From a survey by M.A. Spender assisted by
Mrs. T.A. Stephenson and E.C. Marchant. 1929
Interior of Mangrove Swamp from photographs by RAAF.

Scale : 1/5000
100 0 200 Feet 400 600 800

Wind observations recorded on a Cup
Anemometer by A.G. Nicholls. The length
of the line on any bearing is the mileage
recorded, and represents the amount
of wind (that is the product of velocity
and the duration of that velocity, over
the whole period of 343 days
1 inch on the diagram represents 10,000
miles of wind.



Outer Rampart Shingle.	Mud . . m
Inner " "	Rhizophora
Shingle	Avicennia
Boulders	Bruguiera etc.
Sand . . s	Dry Vegetation
"Honeycomb Rock"	Sesuvium
Coral . . crl	Moats & standing water.
Basset Edges & Beach Rock	Sea

Soundings and heights in feet g.. gravel

DESCRIPTION OF PLATE II.

Chart of Three Isles.

QUEENSLAND

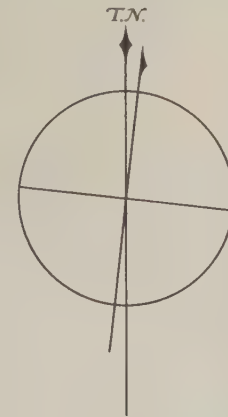
THREE ISLES

Lat. 15°07' S. Long. 145°25' E.

From a survey by M.A. Spender
and Mrs. T. A. Stephenson. May, 1929.

Scale: 1/5000

100 0 200 400 600 800 Feet



Rampart Shingle . . .		Rhizophora	
Shingle		Avicennia	
Shingle and Mud . . .		Dry Vegetation	
Mud		Basset Edges	
Boulders		"High Promenade" . . .	
Sand		"Low Promenade" . . .	
"Honeycomb Rock" . .		Moats & standing water	
Coral		Sea	
Palms			

DESCRIPTION OF PLATE III.

LOW ISLES.

FIG. 1.—Aerial view of the Low Isles reef, from the westward. The several parts of the reef may be identified by comparison with the coloured map (Plate I). On the cay, the lighthouse and the roofs of the four huts used by the expedition can be seen. The dark patches in the *Fungia* moat, and between *Asterina* Spit and the boulder tract, represent areas of coral platform. The sketch was made from a photograph by F. S. Russell, taken from a R.A.A.F. aeroplane, in September 1928.

FIG. 2.—From a second aerial photograph by F. S. Russell, showing the part of the reef concealed by the mangrove swamp in fig. 1. The parts may be identified by reference to Plates I and XXVII. The line representing the seaward edge of the reef is approximate here, as part of it was blurred in the photograph.

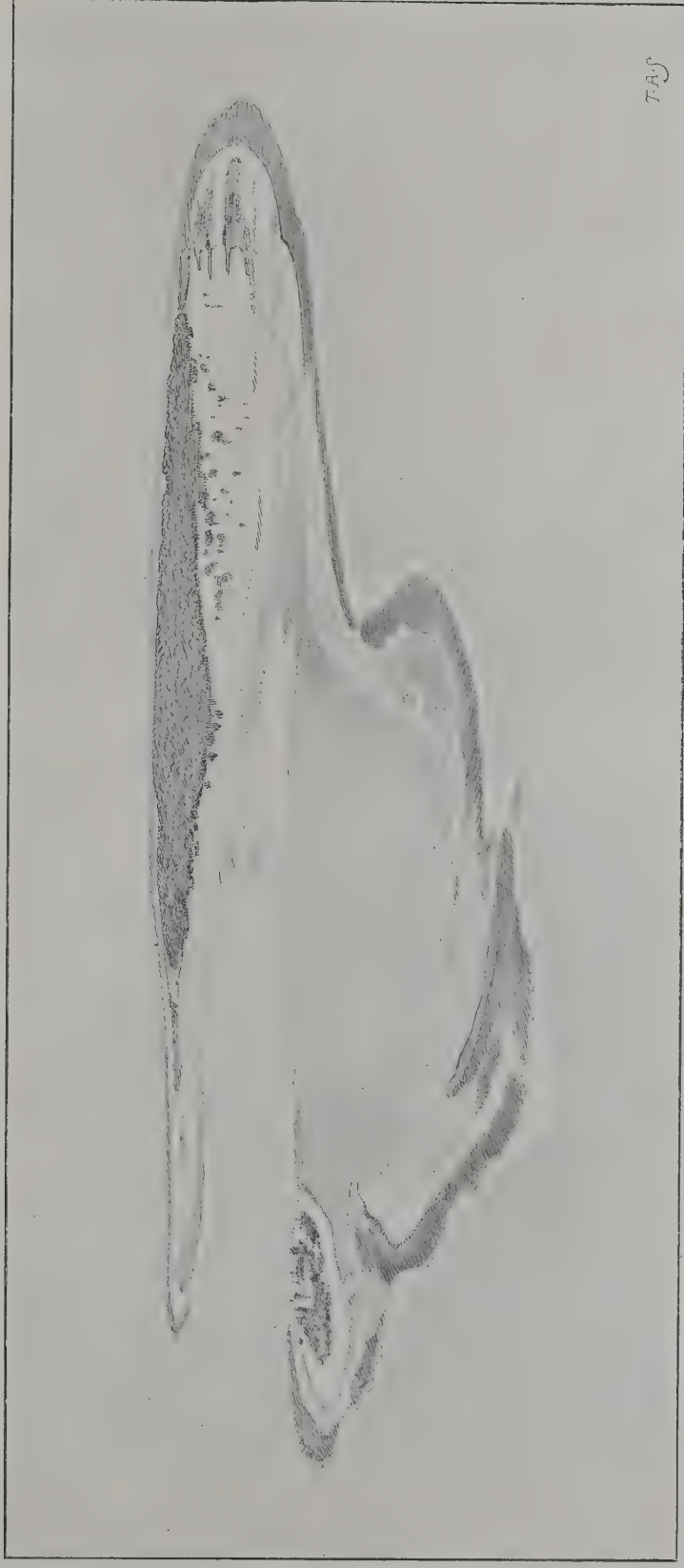


Photo F. S. Russell.

FIG. 1.

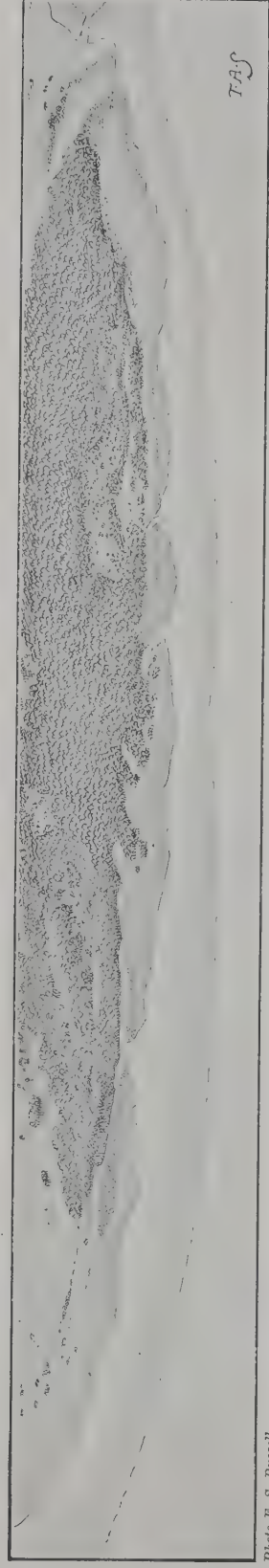


Photo F. S. Russell.

FIG. 2.

DESCRIPTION OF PLATE IV.

LOW ISLES.

FIG. 1.—The cay, viewed across the flat at low water, from the western moat. In the foreground the greater part of the moat is occupied by platforms of massive *Porites*, with small pools between. The stakes and wires in the foreground belong to an enclosure made for ecological observations. Those in the middle distance belong to an enclosed pool in which a coral-growth experiment was carried out. The trees visible on the cay are coconut palms, *Terminalia Catappa* and *Casuarina equisetifolia*.

FIGS. 2-4.—These figures illustrate the development of the mangrove *Rhizophora mucronata*. Fig. 3 shows a bunch of seedlings still attached to a twig of the parent tree; the seeds have germinated, and the long green hypocotyls are seen in several stages of development. In fig. 4 a young seedling has established itself in the sand, and in fig. 2 a somewhat older one, growing in the mangrove park, has developed some stilt-roots. In fig. 4 the stilt-roots of adult trees are shown in the background. The grass-like growth in the foreground of fig. 2 is *Thalassia Hemprichii*.



Photo S. M. Manton.

FIG. 1.



Photo S. M. Manton.

FIG. 2.



Photo G. Tandy.

FIG. 3.

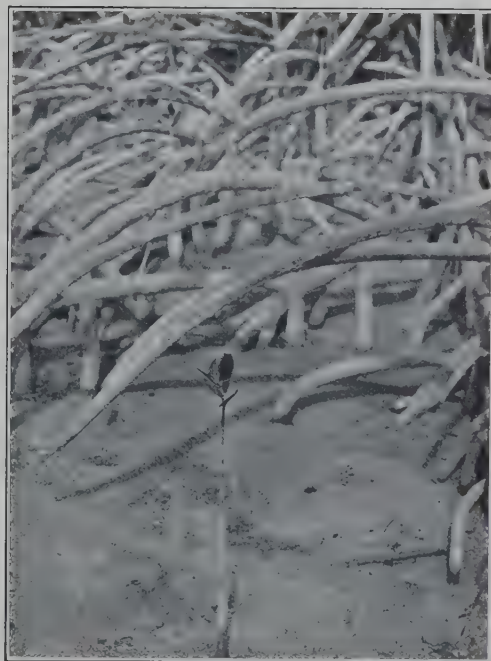


Photo S. M. Manton.

FIG. 4. *Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE V.

LOW ISLES.

- FIG. 1.—General view of the mangrove swamp from the top of the lighthouse. Between the shore of the cay (in the foreground) and the swamp lies the anchorage, and in it are seen the reefs marked A4 on the key chart. The time is low water of a spring tide. Fringing the sand of the cay, on the left, is some beach sandstone (C4 and 6). The trees are *Terminalia* and *Casuarina*.
- FIG. 2.—Part of the principal mass of beach sandstone (C6) viewed at close quarters. The loose blocks in the foreground were broken away artificially.
- FIG. 3.—Part of the boulder tract near the letters B2 on the key chart.
- FIG. 4.—A large boulder on the seaward side of the boulder tract. This is the boulder described on p. 36, and the photograph shows the dense masses of rock-oysters (*Ostrea mordax*) which cover its upper part, and the sharp lower limit to which they extend.

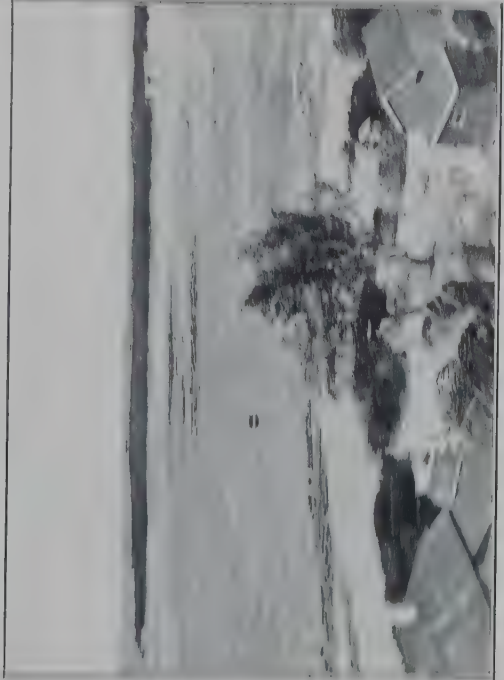


Fig. 1

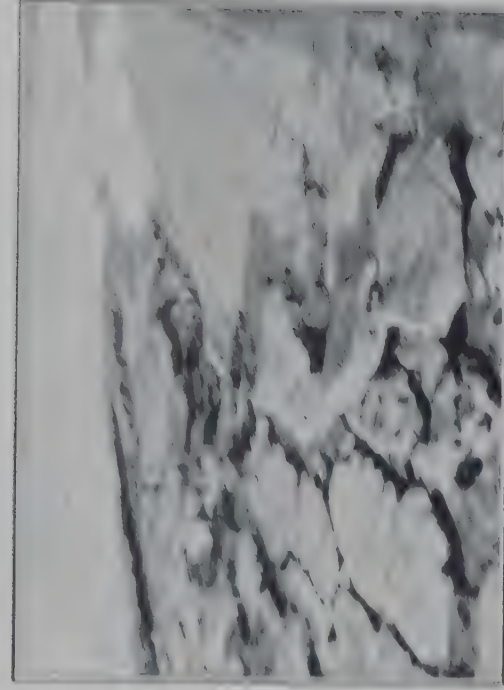


Fig. 2

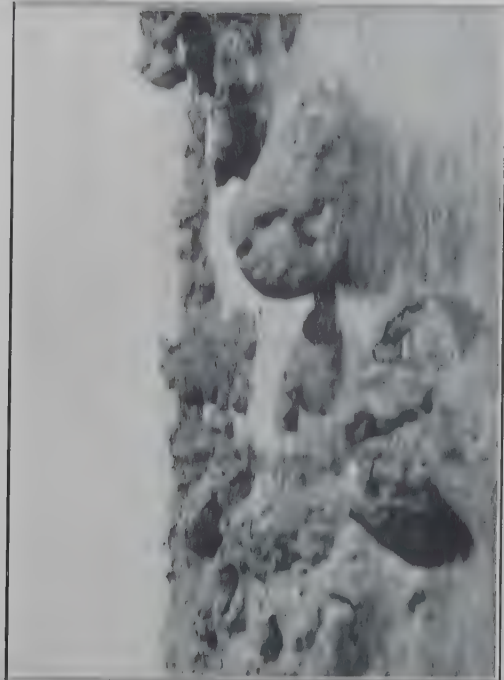


Fig. 3



Fig. 4

DESCRIPTION OF PLATE VI.

LOW ISLES.

- FIG. 1.—The muddy glade IM5, in the mangrove swamp, viewed from the edge of the inner rampart at the time of low water. The trees are mostly *Rhizophora*, but there is one small *Avicennia*. The floor is black mud.
- FIG. 2.—The muddy glade IM4, viewed from the shingle-spit IM4B. The whelks which abound on the mud are *Telescopium telescopium* and *Pyrazus palustris*.
- FIG. 3.—Detail of part of a boulder in the boulder tract, showing a number of colonies of a zoanthid belonging to the genus *Palythoa*, exposed in the sun during low water, and two specimens of the boring clam *Tridacna crocea*, partly buried in the rock.
- FIG. 4.—Part of a boulder close to the one illustrated in fig. 3, showing five specimens of *Tridacna crocea*, more completely buried than those shown in fig. 3. The mouths of the burrows of other boring forms are also visible.



Photo T. A. Stephenson.

FIG. 1.

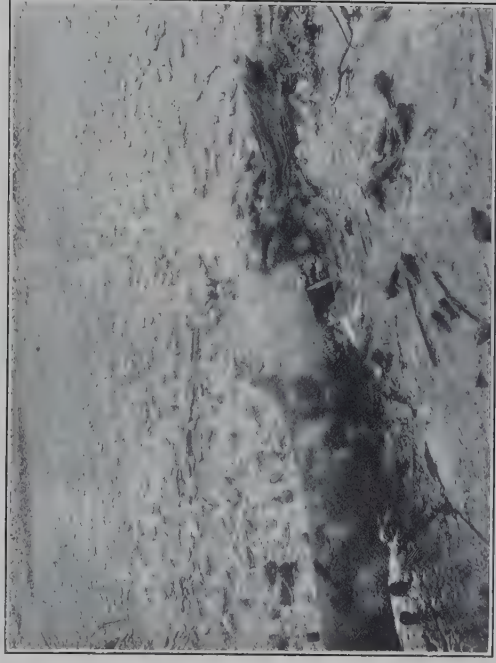


Photo T. A. Stephenson.

FIG. 2.



Photo T. A. Stephenson.

FIG. 3.



Photo T. A. Stephenson.

FIG. 4.

DESCRIPTION OF PLATE VII.

LOW ISLES AND DAINTREE RIVER.

- FIG. 1.—The vegetation on Green Ant Island; typical dry-land scrub, contrasting with the mangrove-vegetation shown in figs. 2-4.
- FIG. 2.—An isolated adult of *Rhizophora mucronata*, in the mangrove park, showing to full advantage the system of stilt-roots.
- FIG. 3.—To show the general aspect of the dense parts of the mangrove swamp. This photograph was taken near the mouth of the Daintree River, on the mainland, but illustrates the nature of the swamp at Low Isles equally well, except that it includes *Bruguiera*, which is strictly localized at Low Isles.
- FIG. 4.—The sandy pool IM1, inside the swamp. This pool contrasts with those illustrated in Plate VI, figs. 1 and 2, in having a sandy floor covered by water at low tide, instead of a muddy floor exposed at low water.



Photo G. Tandy.

FIG. 1.

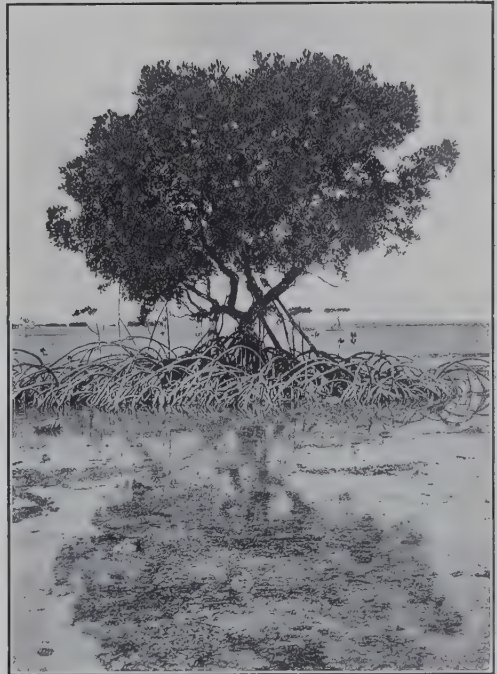


Photo S. M. Manton.

FIG. 2.



Photo S. M. Manton.

FIG. 3.



Photo T. A. Stephenson.

FIG. 4. *Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE VIII.

LOW ISLES.

- FIG. 1.—General view of the sand flat, looking towards the western corner of the reef, with parts of the Thalamita flat, rampart, and boulder tract in the middle distance, and the mainland behind. On the sand are seen numerous mats of the blue-green algae *Lyngbya majuscula* and *Hormothamnium solutum*.
- FIG. 2.—Shallow moat-pools just inside the edge of the outer rampart. The post on the rampart is C beacon (see coloured map).
- FIG. 3.—The madreporo moat, near the gap C, looking seaward. The moat here is occupied by extensive platforms of *Acropora hebes*. The tips of the branches, although they are exposed at low water, are mostly alive in this part of the moat.
- FIG. 4.—A disc-shaped boulder formed by the lateral extension of a colony of massive *Porites*, in shallow water. It is dead except round the edges, and is much encrusted by other organisms.



Photo G. Tandy.

FIG. 1.



Photo M. A. Spender.

FIG. 2.

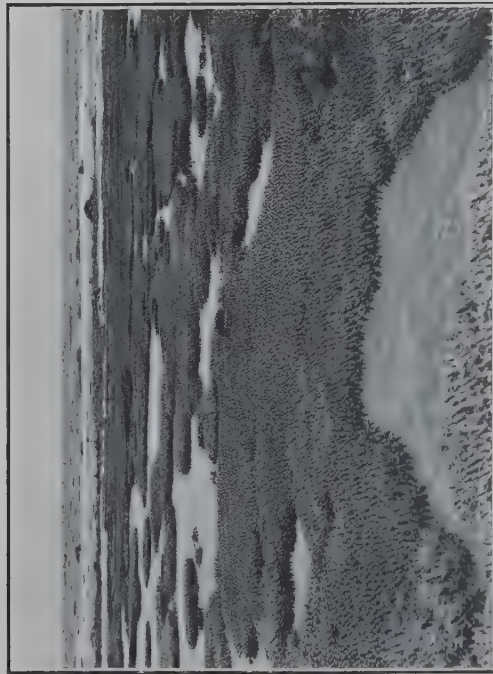


Photo T. C. Roughley.

FIG. 3.

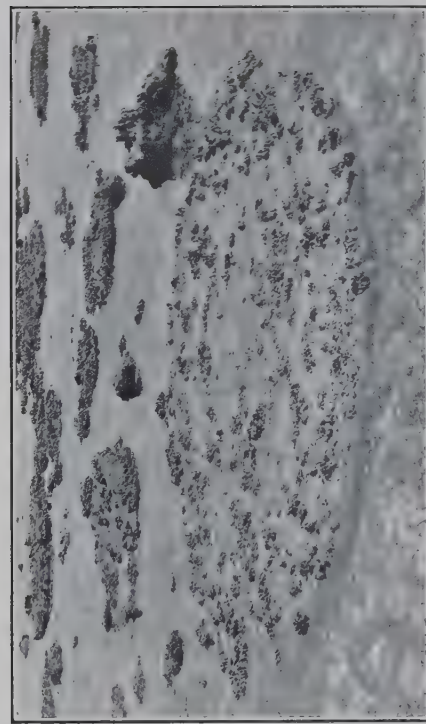


Photo M. A. Spender.

FIG. 4.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE IX.

LOW ISLES.

FIG. 1.—The formation of platforms of *Montipora ramosa* in the western moat (see p. 47).

FIG. 2.—Bushes of a coral (*Acropora pulchra*) which is characteristic of a given level on the reef, occurring in situations open to the sea and just above datum level. These bushes were on the seaward side of the area A1 of Luana Reef. The pale organism in the pool is a fleshy alcyonarian (a species of *Sinularia*).

FIGS. 3 and 4.—Details of the coral growth in the western moat. Fig. 3 shows a good deal of dead rock; *Favias*; a *Coeloria*; colonies of *Acropora* (some alive, the rest dead and encrusted); a fringe of living massive *Porites* round the edge of a dead platform; a little foliose *Montipora*; and a small clam. Fig. 4 includes a *Fungia* and a considerable area of *Montipora ramosa* as well as other elements.



Photo T. A. Stephenson.

FIG. 1.

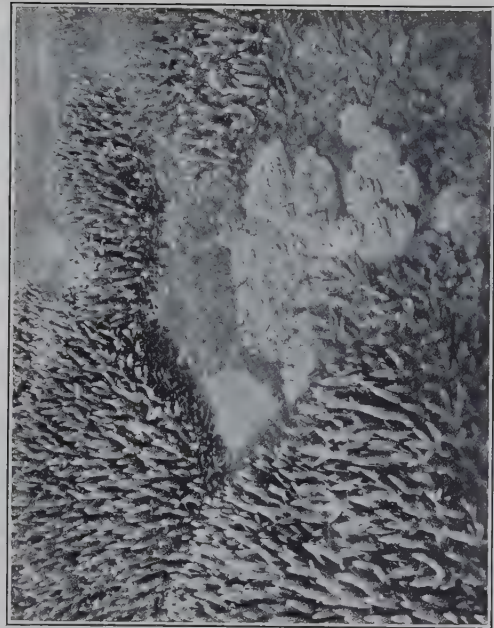


Photo T. A. Stephenson.

FIG. 2.

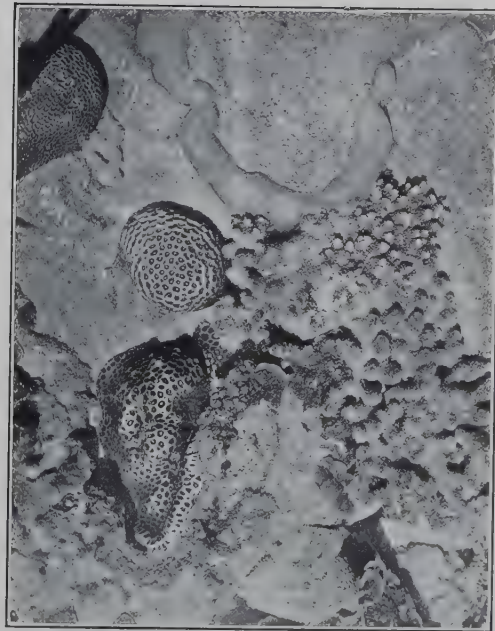


Photo S. M. Manton.

FIG. 3.

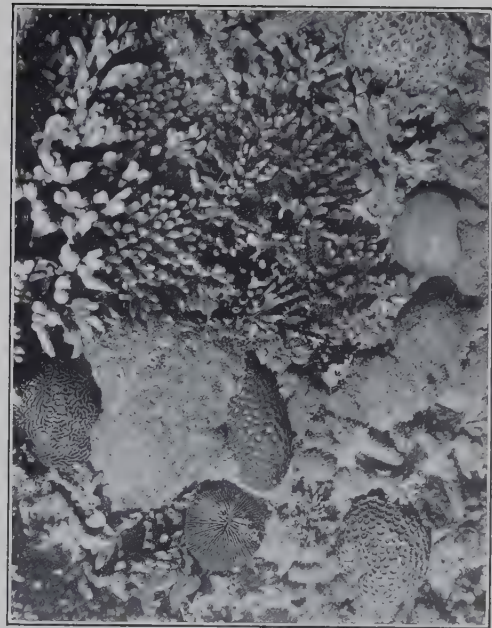


Photo S. M. Manton.

FIG. 4.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE X.

LOW ISLES.

- FIG. 1.—Western moat. Part of a living platform of *Montipora ramosa* with a dark blue specimen of *Stoichactis kenti*.
- FIG. 2.—*Synapta maculata* (above); head-end of a large specimen, with tentacles expanded; and *Linckia laevigata* (below).
- FIG. 3.—In the moat-pool M7. The urchin is *Echinometra mathaei*, the coral *Montipora ramosa*. Note the small polyps of the latter (visible as a honeycomb pattern), fully expanded in sunlight.
- FIG. 4.—Detail of the top of a platform (in a moat) of branched coral. Much of the coral is dead, and is encrusted by *Melobesia* and other algae. The grass-like leaves belong to *Thalassia Hemprichii*.



Photo S. M. Manton.

FIG. 1.



Photo S. M. Manton.

FIG. 2.



Photo T. A. Stephenson.

FIG. 3.



Photo G. Tandy.

FIG. 4. *Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE XI.

LOW ISLES.

- FIG. 1.—General view of a portion of the outer rampart, and of the seaward end of the moat-pool M7, looking southward.
- FIG. 2.—The shingle-tongue R5 and the moat-pool M8. Note the steep slope of the shingle escarpment, and the seedlings of *Rhizophora* which have colonized it.
- FIG. 3.—Part of the outer rampart shown in detail. The fragments are all loose. Note the predominance of stick-like pieces belonging to species of *Acropora*.
- FIG. 4.—Showing the encroachment of the dead shingle of the rampart (in the lower part of the figure) upon living coral in the moat.



Photo T. A. Stephenson.

FIG. 1.



Photo T. A. Stephenson.

FIG. 2.



Photo T. A. Stephenson.

FIG. 3.



Photo M. A. Sponder.

FIG. 4.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XII.

LOW ISLES.

- FIG. 1.—A view of the inner rampart, looking northward from near the shingle-tongue R6. In the foreground on the right is part of the outer rampart, with its escarpment, and here a new wave of clean shingle is clearly seen encroaching upon the older and dirtier shingle. The bush in the centre of the photograph is the one mentioned on p. 57. The mangrove swamp is on the left.
- FIG. 2.—The shingle mound and part of the north-east moat.
- FIG. 3.—A bush of *Avicennia officinalis* growing on the inner rampart, and showing the characteristic form of growth in this position. Note the pneumatophores growing upward from the substratum.
- FIG. 4.—Part of the inner rampart near the south-eastern extremity of the reef, showing a field of *Sesuvium Portulacastrum*. The bushes on the left are *Rhizophora mucronata*.



Photo G. Tandy.

FIG. 1.



Photo M. A. Sponder.

FIG. 2.



Photo S. M. Manton.

FIG. 3.

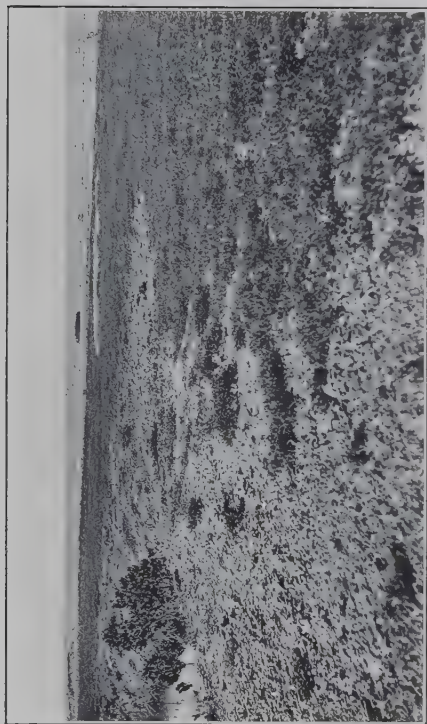


Photo S. M. Manton.

FIG. 4.

DESCRIPTION OF PLATE XIII.

LOW ISLES.

- FIG. 1.—Two shingle-tongues belonging to the outer rampart (the more distant one is the tongue R2 of the key chart), which have encroached upon the inner rampart.
- FIG. 2.—A semicircular bank of loose shingle which has been piled up at the inner side of the inner rampart, opposite the place marked R3 on the key chart.
- FIG. 3.—Inner edge of the inner rampart, in the northern part of its course, showing dead and dying trees of *Rhizophora*, which are now situated outside the swamp, and which appear to have succumbed to unfavourable conditions.
- FIG. 4.—A corner of the mangrove park—the pool P10 in the foreground, and the escarpment of the inner rampart on the left.



Photo T. A. Stephenson.

FIG. 1.

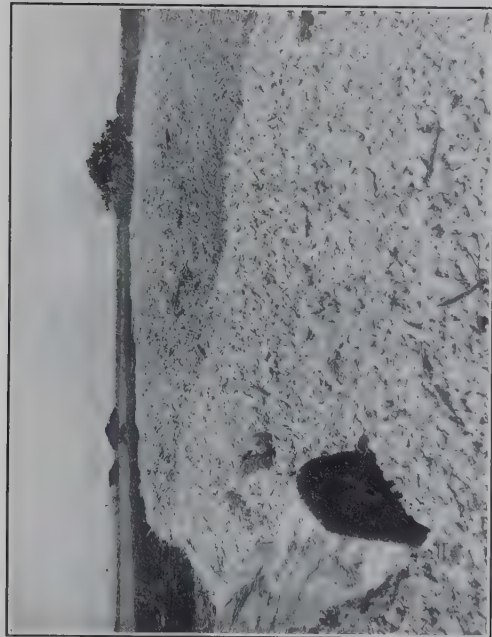


Photo T. A. Stephenson.

FIG. 2.

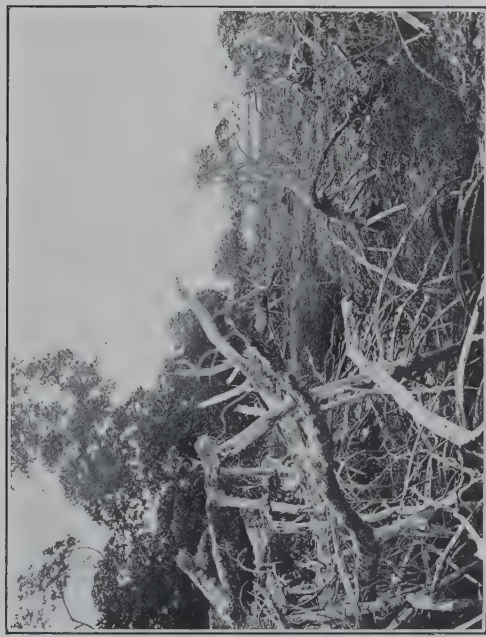


Photo G. Tandy.

FIG. 3.



Photo T. A. Stephenson.

FIG. 4.

DESCRIPTION OF PLATE XIV.

LOW ISLES.

FIG. 1.—Part of the anchorage, viewed from the top of the lighthouse. In the foreground is some beach sandstone, and beyond this the region A1 of Luana Reef. The island-like reef farther away is A3. For further explanation see p. 62.

FIG. 2.—Part of an anchorage reef at close quarters, showing a considerable growth of coral. Among the corals may be seen cyathiform growths of *Acropora*, as well as stagshorn and bush-like species; a colony of *Lobophyllia*; and forms of *Montipora*. There are also alcyonaria (*Sarcophytum* and *Simularia*).

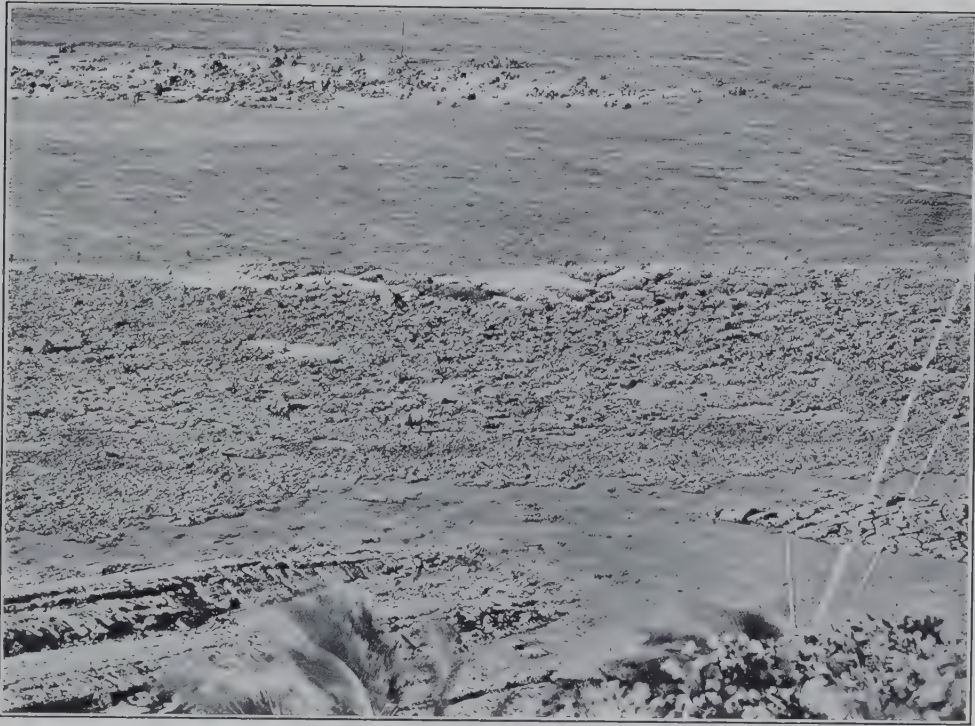


Photo M. A. Spender.

FIG. 1.

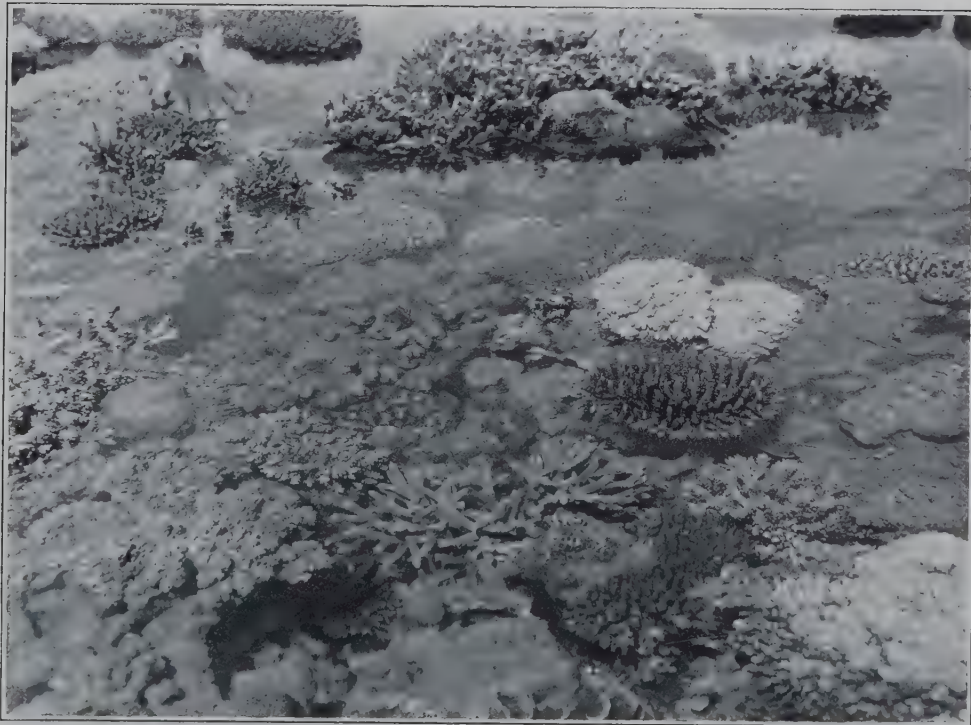


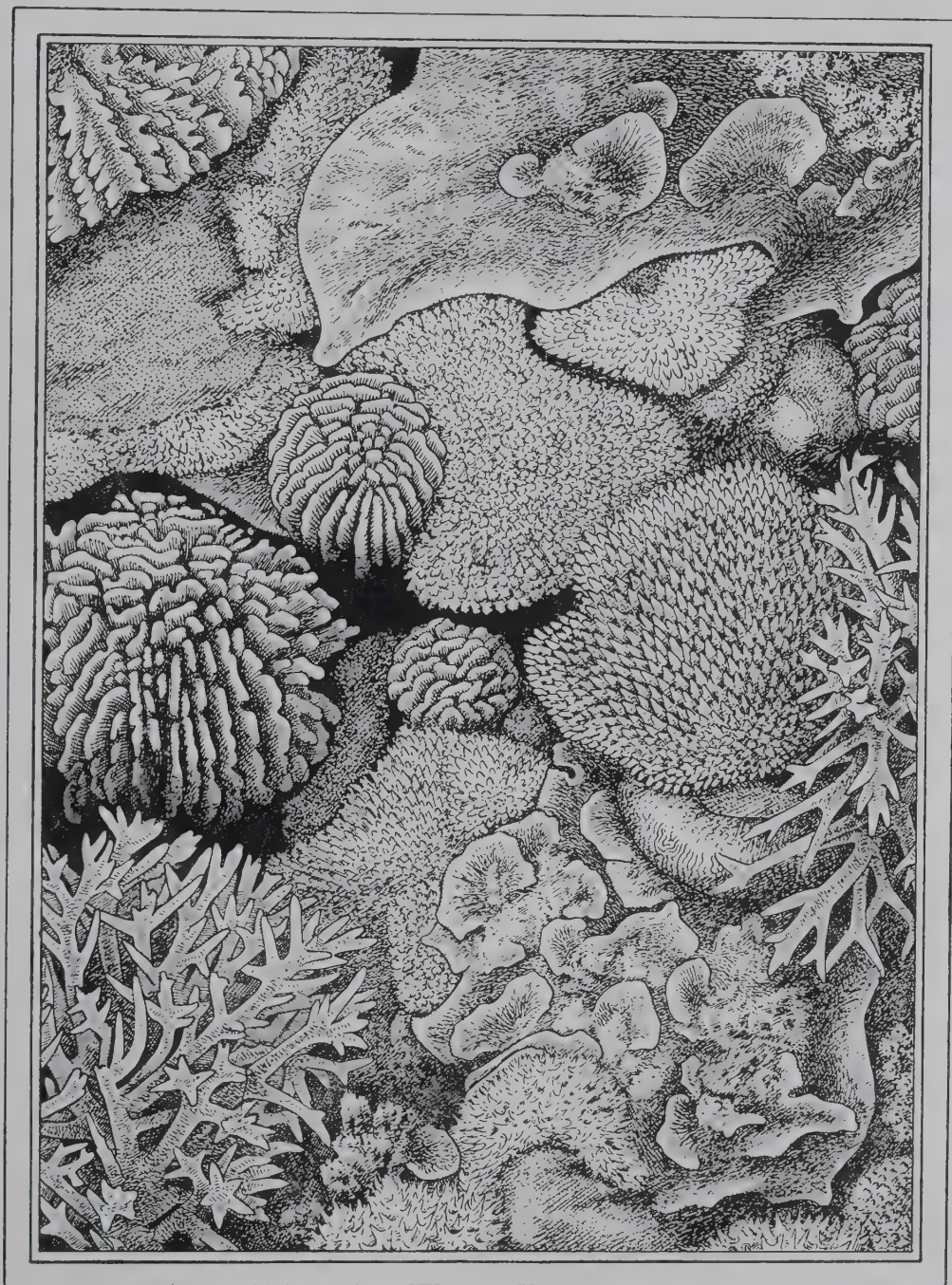
Photo T. C. Roughley.

FIG. 2.

DESCRIPTION OF PLATE XV.

LOW ISLES.

A partially diagrammatic drawing of an area of rich coral growth in the anchorage, towards the edge of the region A2 of Luana Reef. The area was about 8 ft. long by 6 ft. wide. The colonies with radiating vertical lamellae are *Heliopora coerulea*; the coxcomb-like formation in the upper left-hand corner is a species of *Lobophytum*. The foliose forms are species of *Montipora*; the bracket-like growths are species of *Acropora* (mostly *A. squamosa* and *A. loripes*); the stagshorn is also an *Acropora*. At the bottom of the drawing are three colonies of *Seriatopora*, with sharply-pointed branches. A colony of *Coeloria*, partly dead on top, is to be seen on the right, overhung by a stagshorn and a bracket-like madrepore.



DESCRIPTION OF PLATE XVI.

ALCYONARIA AT LOW ISLES.

- FIG. 1.—A large colony of *Sarcophytum*, under water. The colour would be yellowish green and the size several feet across.
- FIG. 2.—Part of a field of *Sinularia flexibilis*, under water, in the anchorage. The "tails" are soft, pale brown, and several inches long.
- FIG. 3.—Fleshy alcyonaria (*Sarcophytum*, *Lobophytum* and *Sinularia*), exposed in the sun at low water, in the region A1 of Luana Reef. The branched coral is *Montipora ramosa*.

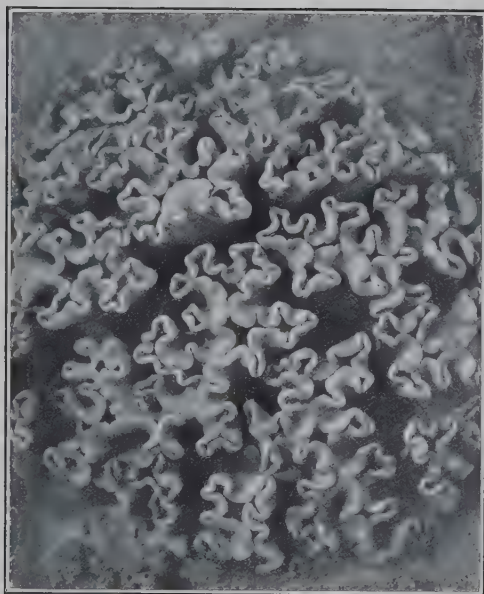


Photo T. C. Roughley.

FIG. 1.

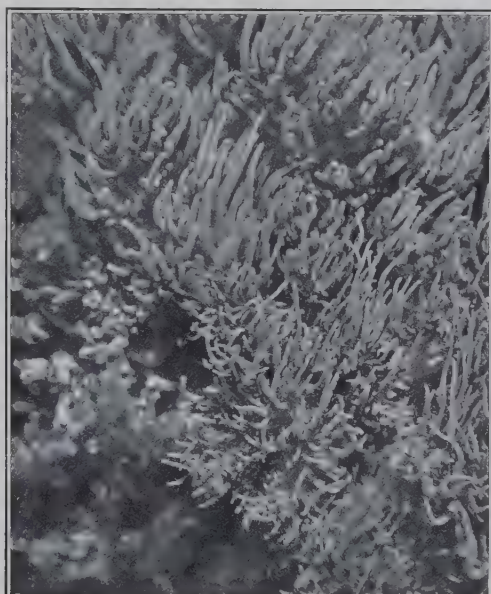


Photo S. M. Manton.

FIG. 2.



Photo T. C. Roughley.

FIG. 3.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XVII.

LOW ISLES AND YONGE REEF.

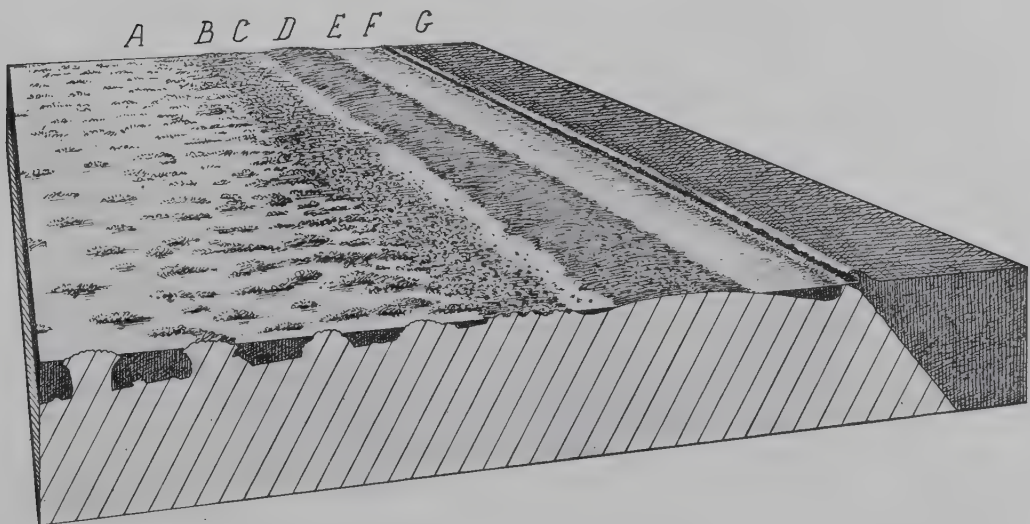
- FIG. 1.—Diagram to illustrate the nature of the seaward slope off the leeward side of Low Isles, and the mode of growth of the coral. In the distance is part of the cay; in front of it a portion of the boulder tract; and in the foreground are two coral heads showing the overhanging form which they often assume, and the manner in which the principal growth of corals is to be found on top of them and a little below the top. In the case of the coral head on the right-hand side of the foreground, the slope from the top of the head to the level of the sea-floor is gradual on one side; and here the rich growth of coral extends farther down than on the overhanging surface. The proportions in this diagram should not be taken too seriously, and it should be compared with Text-fig. 10 and with the text (p. 65). The time is that of low water of a low spring tide.
- FIG. 2.—Diagram to illustrate the arrangement of the several zones on Yonge Reef. This should be compared with the text (p. 30) and with Text-fig. 5. The figure is drawn as far as possible to scale, the vertical scale being 10 times the horizontal; but the coral heads are exaggerated in horizontal scale in order to avoid giving a false impression of their shape. Here also, the time is that of low water of a low spring tide.



T.A.S. del.

FIG. 1.

<i>A</i> "ANCHORAGE" CORAL	<i>E</i> OUTER MOAT
<i>B</i> BOULDER ZONE	<i>F</i> OUTER RIDGE
<i>C</i> INNER MOAT	& BREAKERS
<i>D</i> REEF CREST	<i>G</i> PACIFIC OCEAN



T.A.S. del.

FIG. 2.

DESCRIPTION OF PLATE XVIII.

FAUNA OF LOW ISLES: CLAMS.

- FIG. 1.—*Hippopus hippopus*. Adult specimen, about a foot long. The adults of this species lie loose on the substratum, anchored only by their own weight.
- FIG. 2.—*Tridacna derasa*. A specimen nearly 2 feet long, in the western moat. The shell is not gaping as widely as it is able to do, because part of the animal is projecting above the water. This species is attached when young, free when adult.
- FIGS. 3 and 4.—Two small clams, both firmly attached to the substratum, and inhabiting the pool M7. The specimens were about 7 inches long, and probably both belong to *Tridacna fossor*. Their mantles illustrate the variation in pattern which is to be found from one specimen to another (see p. 48).



Photo T. A. Stephenson.

FIG. 1.



Photo T. A. Stephenson.

FIG. 2.



Photo T. A. Stephenson.

FIG. 3.



Photo T. A. Stephenson.

FIG. 4. *Adlard & Son, Ltd., Impr.*

DESCRIPTION OF PLATE XIX.

FLORA OF LOW ISLES.

FIG. 1.—A typical growth of the flowering plant *Thalassia Hemprichii*, heavily colonized by the foraminiferan *Orbitolites complanata*.

FIG. 3.—The fleshy plant *Sesuvium Portulacastrum*, growing on the inner rampart.

FIGS. 2 and 4.—These figures illustrate the algal growth in the “trickle-zone” of the outer rampart, and also a certain degree of binding of the shingle by non-calcareous algae. Fig. 4 shows an almost pure growth of *Caulerpa racemosa*, fig. 2 a mossy algal turf chiefly composed of other forms.

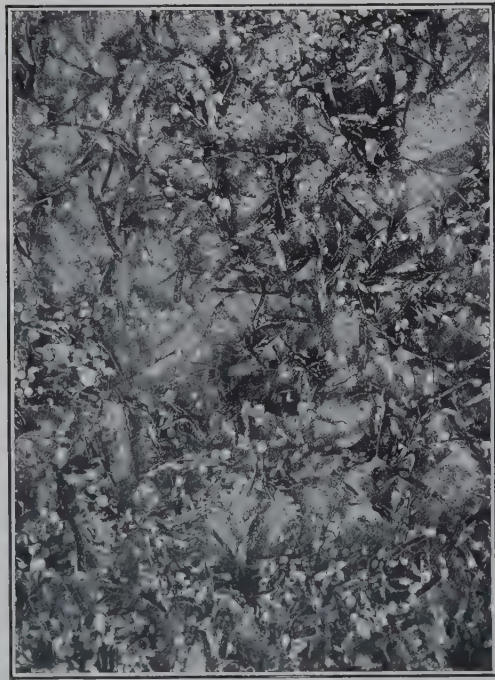


Photo S. M. Moulton.

FIG. 1.

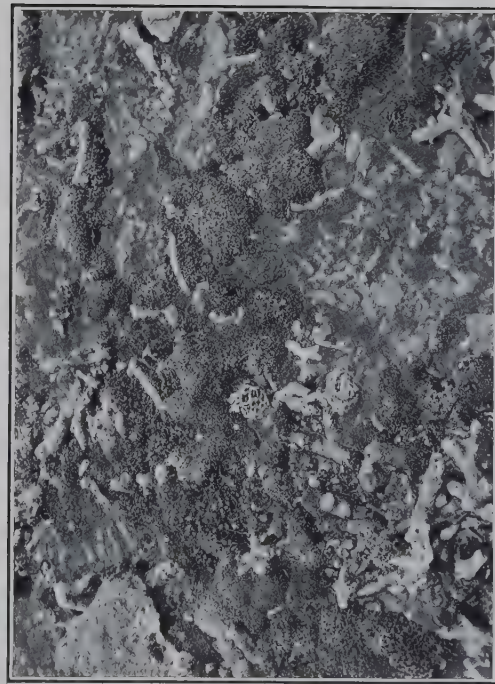


Photo G. Tandy.

FIG. 2.



Photo G. Tandy.

FIG. 3.

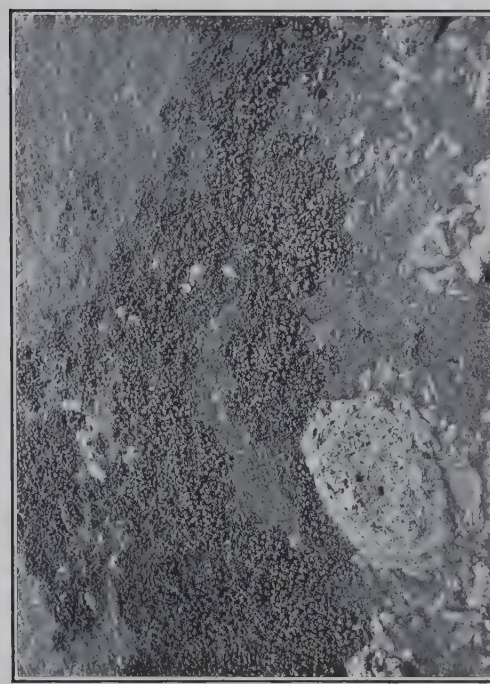


Photo G. Tandy.

FIG. 4.

Allard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XX.

FAUNA OF LOW ISLES.

- FIG. 1.—The anemone *Actinodendron plumosum*. The body is buried in sand; the oral disc is produced into arms bearing branched tentacles. The animal was about 8 inches in diameter, and was coloured bright reddish brown.
- FIG. 2.—A colony of the urchin *Centrechinus* (*Diadema*) *setosus*, living in a moat. The individual urchins are about a foot across, and coloured deep purplish black. The pale spots visible on them in the photograph are in reality bright blue. The corals are massive *Porites*, *Pocillopora*, etc.

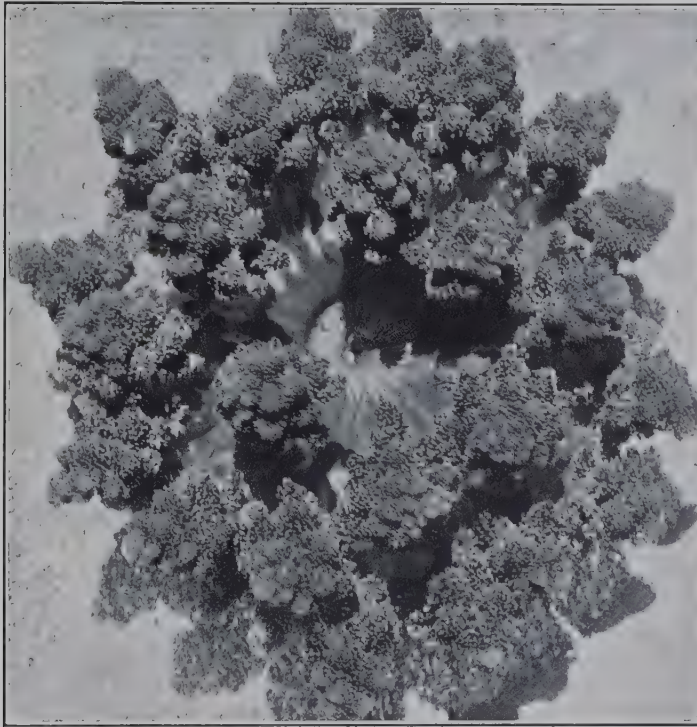


Photo T. A. Stephenson.

FIG. 1.

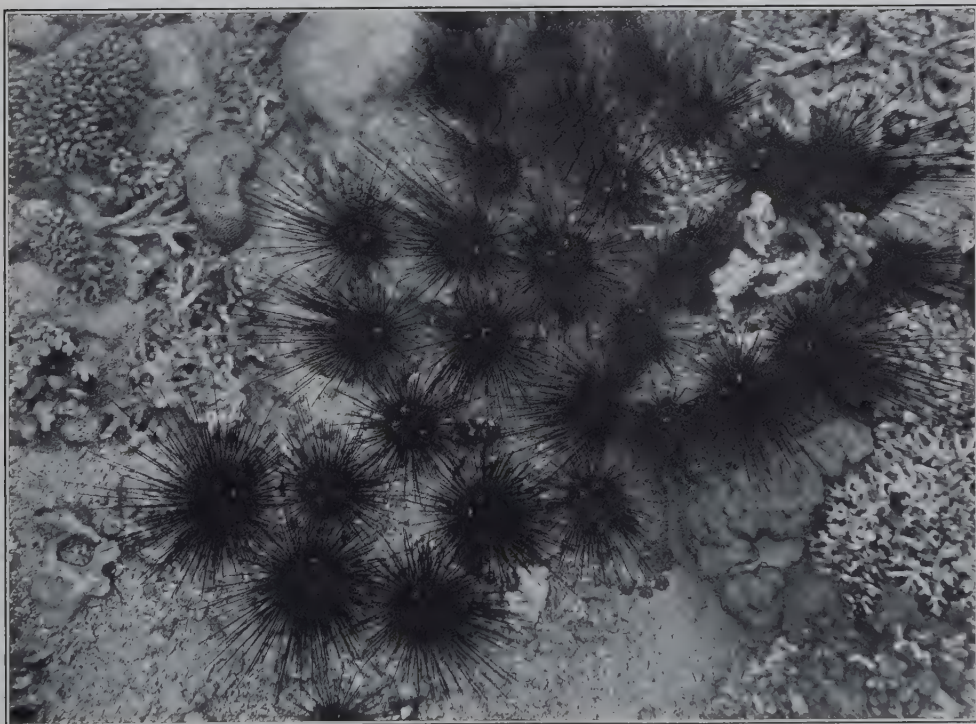


Photo T. C. Roughley.

FIG. 2.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XXI.

FAUNA AND FLORA OF LOW ISLES.

FIG. 1.—The convolvulus *Ipomaea Pes-caprae*, on the cay.

FIG. 2.—The chiton *Acanthozostera gemmata*, in the boulder tract. The length of the specimen was about 5 inches. The holes of boring organisms are also visible.

FIG. 3.—The baler *Melo diadema*, in the act of producing its egg-mass. The shell of this gastropod attains a length of 9 inches or more.

FIG. 4.—A colony of Zoanthids growing on a mangrove root, in the pond RP3. This species is common on the roots of *Rhizophora*. The polyps, which are half an inch or more in diameter, when in the condition here shown, are partly contracted because of the strong sunlight, although they are under water.



Photo G. Tandy.

FIG. 1.



Photo T. A. Stephenson.

FIG. 2.



Photo G. Tandy.

FIG. 3.



Photo T. A. Stephenson.

FIG. 4.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XXII.

THREE ISLES.

- FIG. 1.—The southern corner of the “high promenade” which lies to seaward of the dune and the mangrove swamp. The substratum in the foreground is “honeycomb-rock” overgrown by algae, etc.
- FIG. 2.—A closer view of the rocky promenade belonging to the Third Island, showing its pitted and eroded surface.
- FIG. 3.—A general view of the dune. The mainland can be seen in the distance (the two mountainous masses being the southern and northern parts of the Cape Bedford Peninsula), and the mangrove swamp would be to the right of the observer.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).

REPORTS, VOL. III, No. 2.

PLATE XXII.

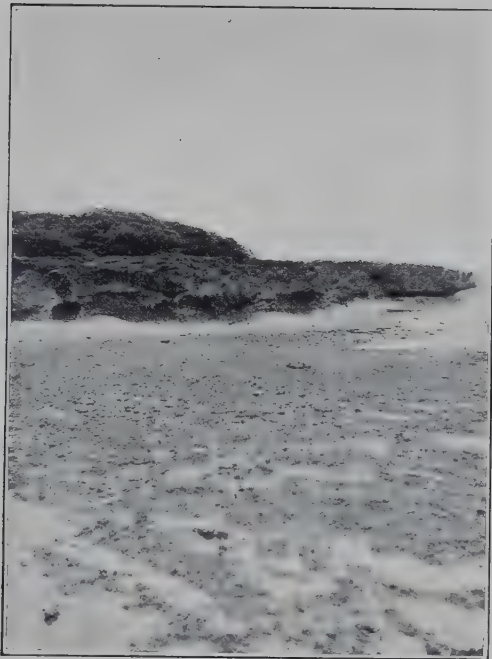


Photo T. A. Stephenson. FIG. 1.



Photo T. A. Stephenson. FIG. 2.



Photo M. A. Spender.

FIG. 3.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XXIII.

YONGE REEF.

- FIG. 1.—The reef-crest viewed from the outer moat. The observer is standing near the outer ridge, the water in the foreground all belongs to the outer moat, and the reef-crest appears as a narrow band with sea beyond it. The distant mountain is one of the Direction Islands.
- FIG. 2.—The outer ridge. The observer is looking towards the Pacific, and towards the line of breakers on the edge of the reef. Between the breakers and the foreground is one of the cleft-like interruptions in the outer ridge mentioned on p. 32.
- FIG. 3.—A general view of a typical portion of the reef-crest, with a very sparse growth of coral.
- FIG. 4.—A portion of the reef-crest where the coral-growth is more prolific than in the part shown in fig. 3. The reef-crest here constitutes the foreground; the pale line behind it is the inner moat, and beyond that a line of boulders belonging to the boulder-zone is visible. The mountains in the distance are Lizard, Newt and Iguana Islands.



Photo T. A. Stephenson.

FIG. 1.

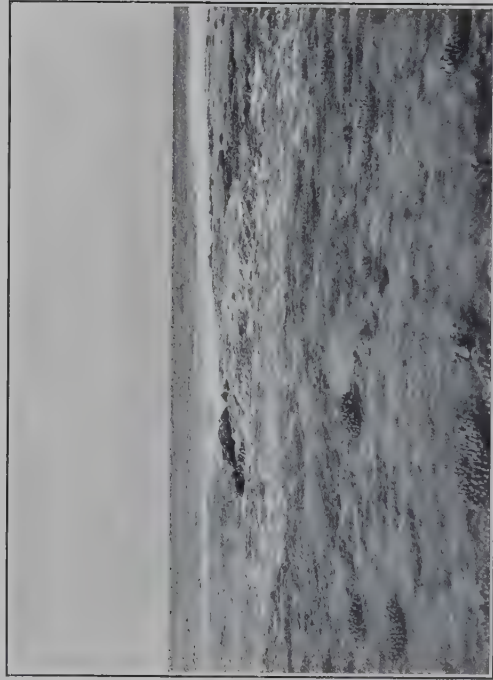


Photo Anne Stephenson.

FIG. 2.

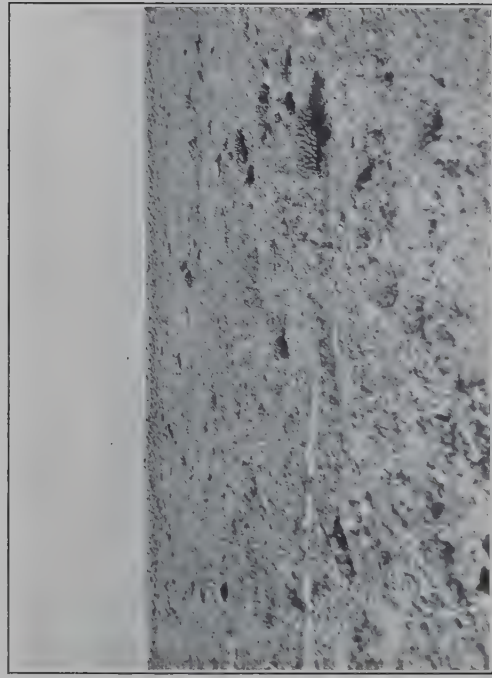


Photo Anne Stephenson.

FIG. 3.



Photo T. A. Stephenson.

FIG. 4.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XXIV.

YONGE REEF.

- FIG. 1.—The anchorage coral zone. The observer is standing on the leeward side of the reef, looking towards the reef-crest.
- FIG. 2.—Coral on one of the table-like "coral-heads" on the leeward side of the reef. The top of a second coral-head, like an island, is seen in the middle distance. Although this looks like a low reef, it is actually the top of a mass of coral with precipitous sides below the water. The channel between the foreground and the more distant coral-head was about three fathoms deep. The coral growth here is of about maximal density, and consists principally of species of *Acropora*, amongst which the bracket-like *A. hyacinthus* and the form with short thumb-like branches (*A. gemmifera*) are conspicuous.

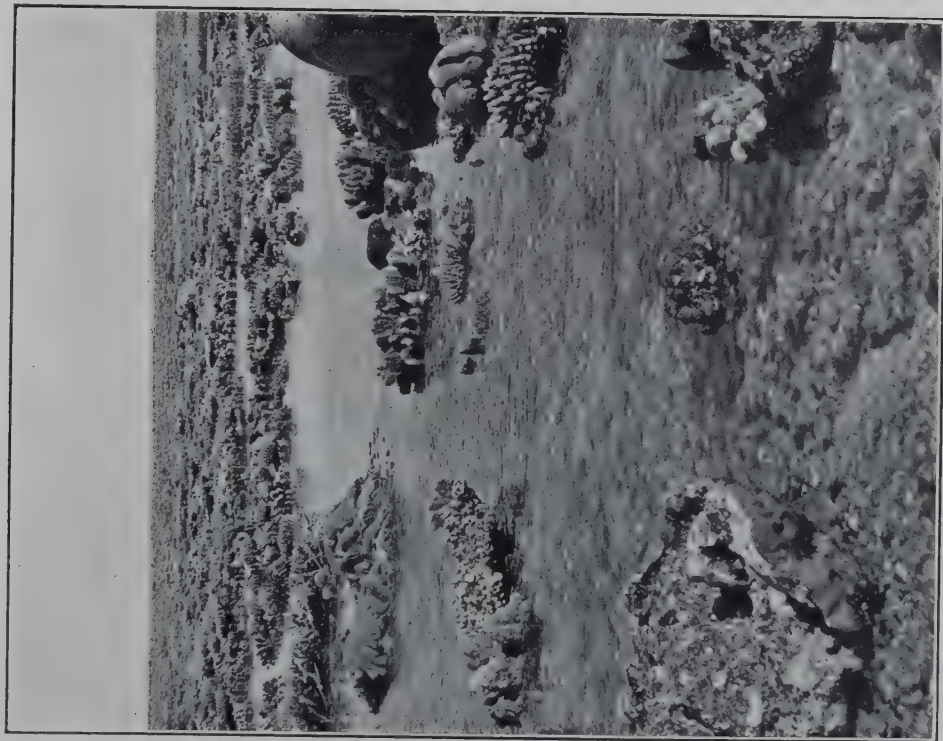


Photo S. M. Manton.

FIG. 1.

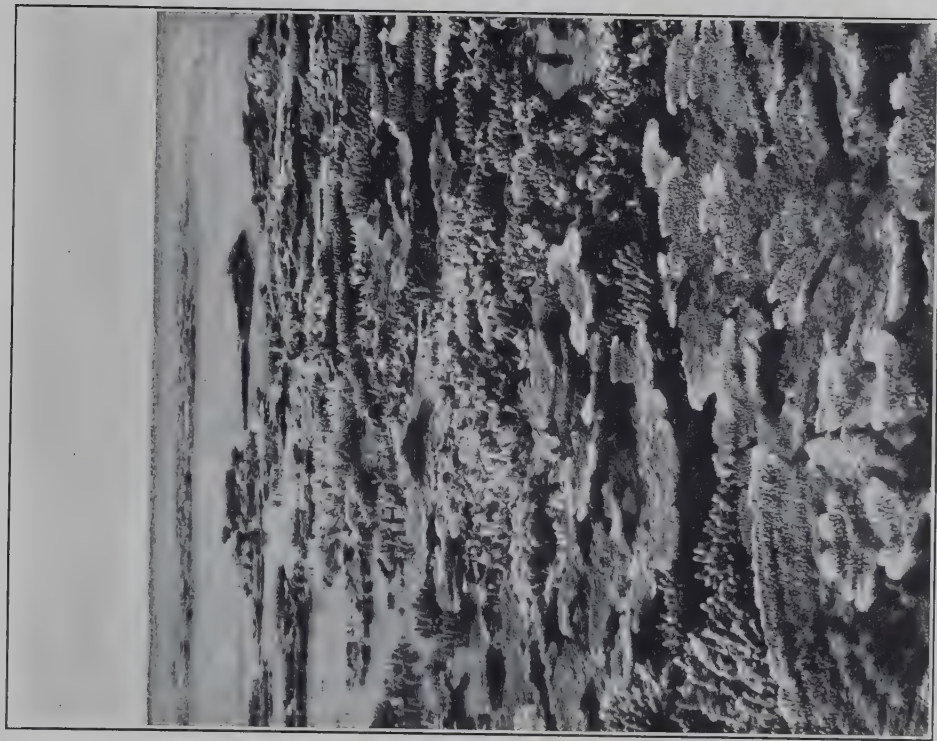
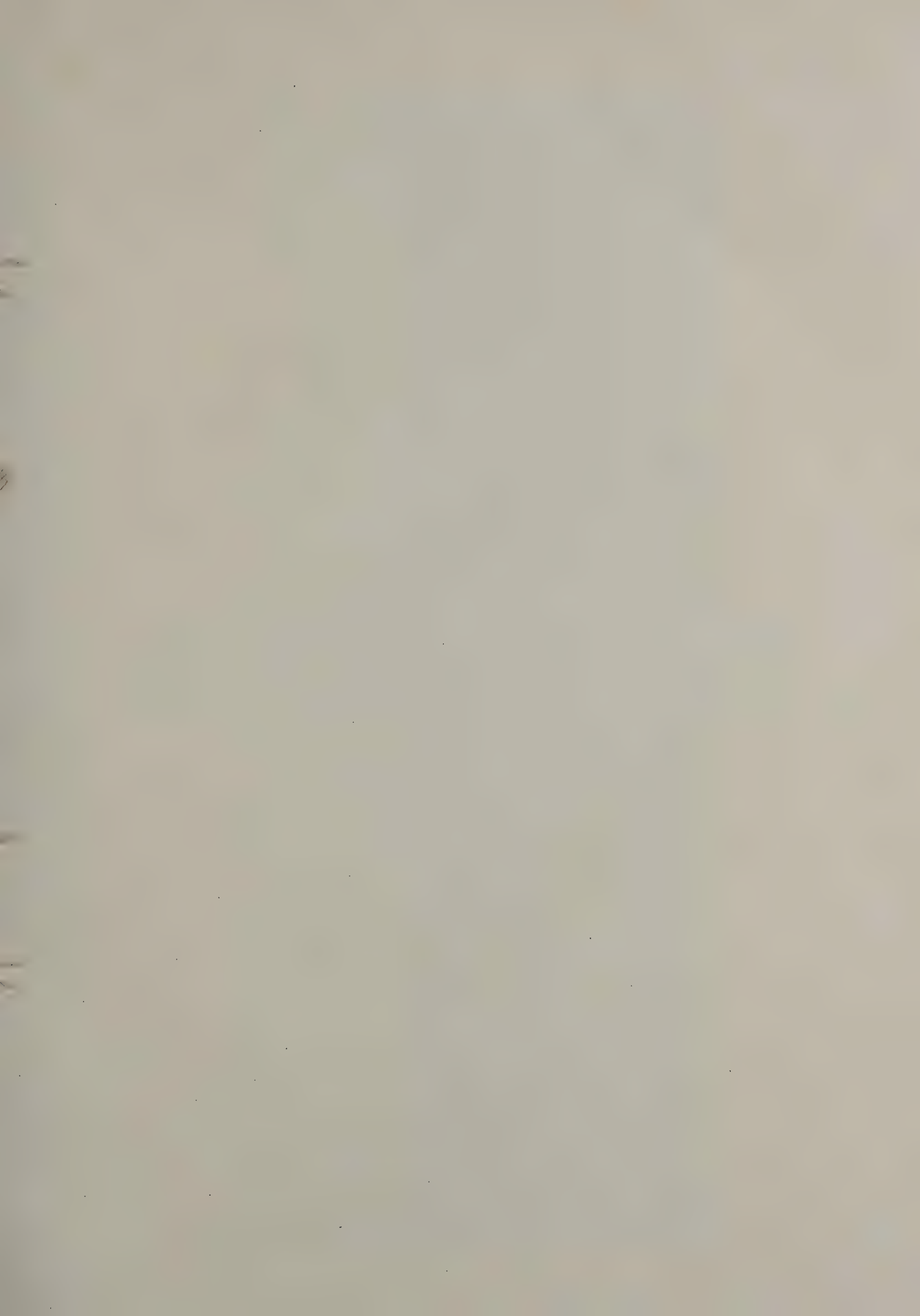


Photo T. A. Stephenson.

FIG. 2.

Adlard & Son, Ltd., Impr.



DESCRIPTION OF PLATE XXV.

LIZARD ISLAND.

A sketch made from near the summit of the island, at a height of some 1100 ft. The foothills of Lizard Island form the foreground; the small islands are Newt and Iguana Islands; and between these and the foreground lies the system of reefs described on p. 87, and further illustrated in Text-fig. 6 and in Pl. XXVI, fig. 3. The three large distant reefs are Eagle Island, M reef, and L reef. In the background is the mainland, Capes Flattery and Bedford being visible. The position of Rocky Islets is indicated just below the horizon on the left.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).

REPORTS, VOL. III, No. 2.

PLATE XXV.



T. A. S. del.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XXVI.

THREE ISLES, ARLINGTON REEF, LIZARD ISLAND AND YONGE REEF.

- FIG. 1.—Three Isles. A general view of the Third Island from its southern end. Three grades of vegetation are distinguishable (approximately). The low bushes in the foreground are mostly *Avicennia*; the darker ones of intermediate height on the left are other bushes (*Pemphis acidula*, *Osbornia octodonta*, or both); the tall trees are *Rhizophora*.
- FIG. 2.—Arlington Reef. A general view of the reef-flat. This photograph is included to illustrate the nature of the flat of a reef belonging to the Inner Series; it might equally well have been taken on Batt Reef.
- FIG. 3.—Lizard Island. View from the western slope of the mountain. Iguana Island is seen on the left, and between this and the foreground lies the western part of the shoal described on p. 87, with a number of reef-patches (clearly visible below the water as dark areas) on its surface.
- FIG. 4.—Yonge Reef. Madrepore field (see p. 84) at the southern end of the reef.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).

REPORTS, Vol. III, No. 2.

PLATE XXVI.



Photo M. A. Spender.

FIG. 1.



Photo M. A. Spender.

FIG. 2.

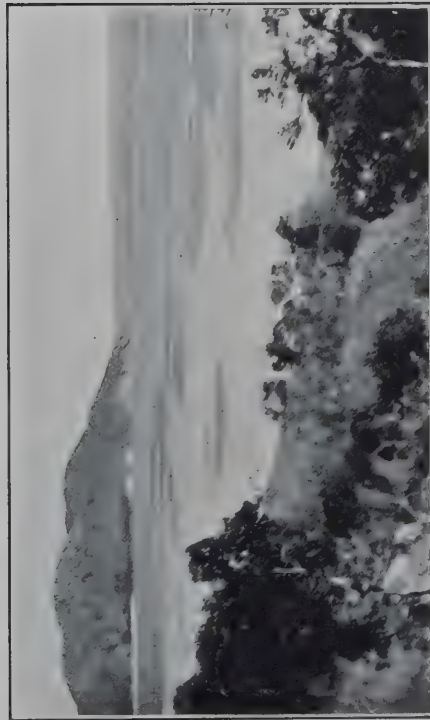


Photo Anne Stephenson.

FIG. 3.



Photo M. A. Spender.

FIG. 4.

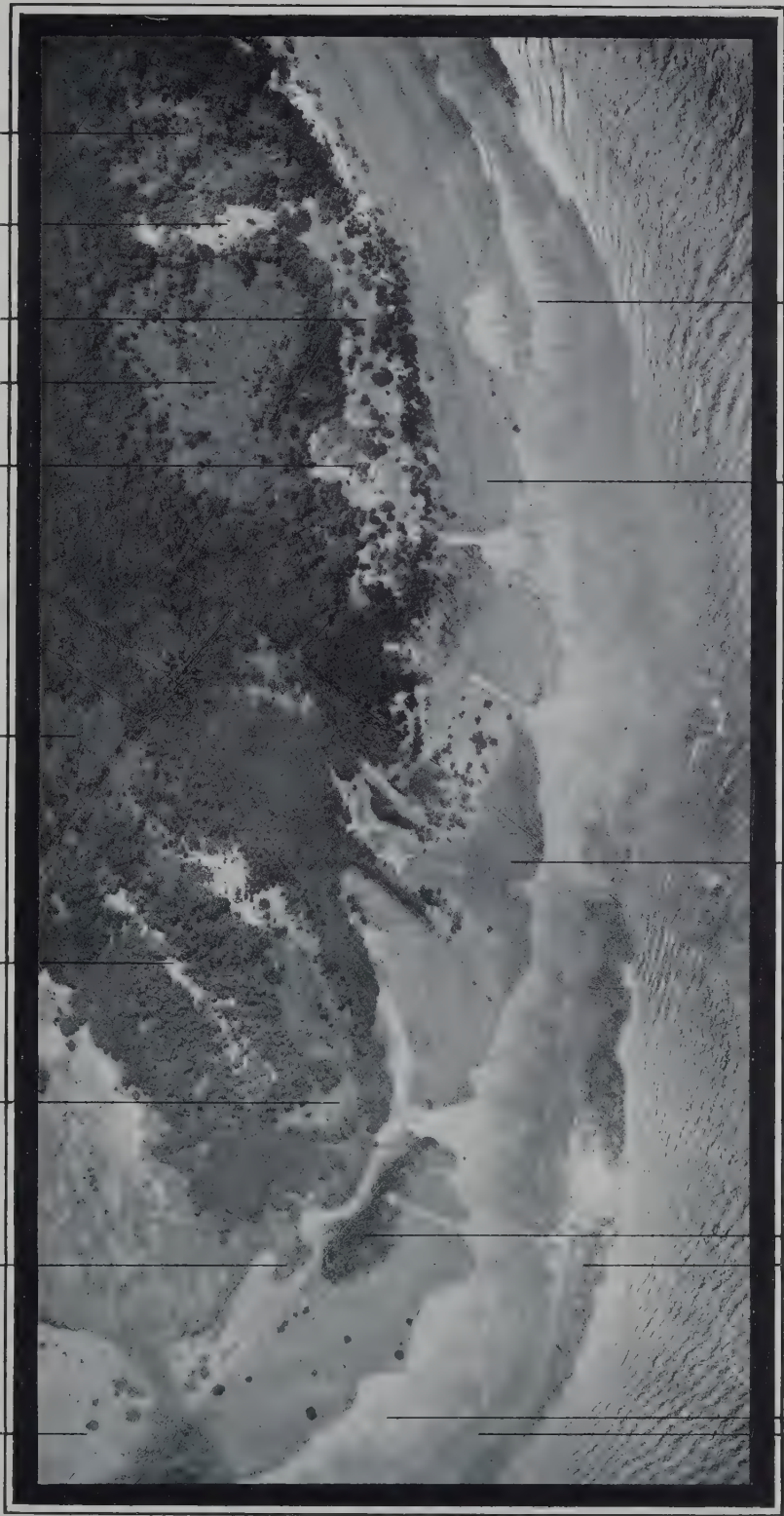
Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XXVII.

LOW ISLES.

A mosaic made from aerial photographs by the R.A.A.F., taken in September, 1928. It illustrates a number of details—the muddy glades in the mangrove swamp; the shingle tongues which also lie in the mangrove swamp; the appearance and relations of the inner and outer ramparts; the distribution of *Sesuvium* and other small vegetation on the inner rampart; the shingle-bank which is compared in the text (p. 96) to the Three Isles dune; the encroachment of the outer rampart upon the inner; the formation of secondary shingle-waves on the outer rampart; the zonation of the outer rampart; the honeycomb rock of the windward shelf; etc.

IR3 P10 IM3 THE LONG TONGUE IM2 GREEN ANT ISLAND IM4 IM4B IM4A IM5



OUTER RAMPART SESUVIUM M7 (POOL) INNER RAMPART NEW SHINGLE-WAVE
TRICKLE ZONE HONEYCOMB ROCK PHOTOGRAPHS BY R.A.A.F.

DEVELOPMENT AND THE FORMATION OF COLONIES IN POCILLOPORA AND PORITES.—PART I

BY

T. A. STEPHENSON, D.Sc.

(Professor of Zoology in the University of Cape Town)

WITH SIXTEEN TEXT-FIGURES AND SIX PLATES

CONTENTS

	PAGE
I. INTRODUCTION	113
II. POCILLOPORA BULBOSA	114
A. The extrusion of planulae	114
B. The method of rearing	116
C. The development of the colony after the attachment of the larva	122
D. The progressive modification of the skeleton	128
III. PORITES HADDONI	129
A. The extrusion of planulae	129
B. The development of the colony after the attachment of the larva	130
IV. THE RESPONSE OF YOUNG COLONIES TO SEDIMENTATION	132
REFERENCES	134

I. INTRODUCTION.

IN his recent account (1929) of the post-larval development of *Macandra* (*Manicina*) *areolata*, Boschma summarizes the data which exist on the development of the Madreporaria; they are strikingly few, and mainly concern the earlier phases. Edmondson, working at the Marine Biological Laboratory of the University of Hawaii, at Waikiki, has recently reared larvae of *Dendrophyllia manni*, *Pocillopora cespitosa*, and *Cyphastrea ocellina*. He has published a short account (1929) of the development of these species, but does not go into detail. Such data as are given with regard to *Pocillopora cespitosa* suggest that many of the details of development in that species are different from those of *P. bulbosa*, as described below.

Matthai, in his notable paper of 1926 on colony-formation in Astraeid corals, remarks (p. 313) that "Colony-formation in the Madreporaria was generally described as taking

place by two principal methods, viz. budding and fission. This statement was based on the study of the hard parts, which were examined without reference to the polyps that formed them"; and later, "it is now clear that no reliable data on colony-formation can be obtained from a study of coralla only," and "stages in the budding of the polyps of *Astraeid* colonies are herein described for the first time." Even with the data obtained by Matthai, added to those available from earlier work (especially from the classical papers of Duerden), we are still limited almost entirely, for our knowledge of budding in the *Madreporaria*, to information procured by examination of young colonies and of the growing regions of older ones, whether externally on living material, or by means of sectioning fixed and decalcified colonies. So far as I am aware, apart from the data given by Edmondson, this paper describes for the first time the budding of reef-corals actually witnessed on the living colony, from the extrusion of the planula onward, over a considerable period of time. This is a little remarkable, in the year 1930, when we consider that even the older text-books speak of asexual reproduction in the *Madreporaria* as if a considerable body of knowledge relating to it were extant; but it is in fact natural enough, because the long residence on a coral reef which is the first condition of its attainment, together with the facilities for rearing larvae, are not everyday occurrences.

In the present paper only the outlines of the story are told; in Part II the anatomical details, together with a discussion, will be provided.

I am very much indebted to F. Pittock (Department of Embryology, University College, London) for the beautiful photomicrographs here reproduced; to Eleanor Dale for two drawings (Plate II, fig. 4, and Plate V, fig. 10); to Joyce Townsend for Text-fig. 1; and to Anne Stephenson for the remaining text-figures. I must also express thanks to F. W. Moorhouse, E. A. Briggs and P. D. F. Murray for very valuable assistance in the construction and planting out of the "clock-towers" described on p. 117, in which the larvae were reared; and to A. G. Nicholls for the planktonic food-supply which was used during the early stages of the work. The information given as to the breeding-seasons of *Pocillopora* and *Porites* is the result of work carried on partly by myself, but also by S. M. Marshall, who made a large proportion of the collections involved.

II. *POCILLOPORA BULBOSA*.

A. THE EXTRUSION OF PLANULAE.

This coral (Plate VI, fig. 9) is a branching species common in the moats at Low Isles. It does not, as a rule, attain a very large size; a colony with a diameter of 15 inches may be regarded as a well-grown specimen. The colour of the soft parts during life is usually yellowish brown of several shades, not varying greatly from one colony to another. The polyps expand during daylight (a somewhat exceptional feature), and their tentacles have knobbed tips, the knobs being frequently pale green.

I have not seen eggs or sperm emitted by any colony of this species; but large and well-developed planulae are readily extruded under certain conditions. The emission of planulae in nature is not a continuous process extending over a single breeding-season in each year, but is intermittent, and is related to phases of the moon. The periods of spawning are related to the time of new moon in the summer, and to that of full moon

in the winter, with a transition-period in May and June. The evidence for this conclusion will be presented in a later paper on the breeding of reef-animals; it is incomplete, but sufficient to justify the conclusion stated.

Planulae may be obtained for rearing by breaking off branches of the coral during a breeding-period, and bringing them home in a bucket of sea-water. Many planulae are



JOYCE
TOWNEND

TEXT-FIG. 1.—Transverse section of a planula of *Pocillopora bulbosa*, fixed shortly after extrusion.

The figure shows the comparatively advanced condition of the free-swimming larva—the specimen in question has already its full complement of mesenteries (six bilaterally arranged couples), three couples of which bear filaments. The endoderm is still in an embryonic condition. $\times 200$.

usually emitted in transit, and others subsequently. They can readily be picked out of the vessel containing the coral, with a pipette, and transferred to finger-bowls for rearing. The first considerable crop observed, from which a number were reared, occurred in December 1928, when some 3,500 were isolated for observation.

The "planulae" (Text-fig. 1) do not deserve their name. They are ciliated, free-swimming larvae, it is true; but in their internal organization are far beyond the stage

to which the term "planula" is strictly applicable among coelenterates. They are, in fact, polyps, but still lack tentacles, and are not yet attached; they have well-developed mesenteries, mesenterial filaments, mouth and throat, and nematocysts of more than one kind. They are large (*e. g.* 1.6 mm. long)—easily visible to the naked eye—opaque cream or light to fairly dark brown in colour, and swim actively in the water at any level in the vessel containing them. The brown colour is due to zooxanthellae within their tissues. Their shape is very variable, both in the same planula and from one to another; but the usual shape is pear-shaped or wedge-shaped, with one end broader than the other. At the narrow end is a spot representing the mouth. Swimming takes place with the aboral end in advance; the forward motion is rapid, and is accompanied by counter-clockwise rotation (viewing the larva from the aboral pole). In some cases the form is so nearly cylindrical that the oral end can only be distinguished by the presence of the mouth. The ectoderm is translucent, the endoderm opaque. The planulae vary considerably in size, although the average is considerably larger than in the case of *Porites haddoni*.

It is a curious fact that any one polyp of the parent colony produces only a single planula at a time, or at most two or three. This is easily verified by studying fertile branches of the coral under a binocular, when the pregnant polyps are easily distinguished, and the contained planulae can be extracted with a needle. The single planula is often nearly as large as the polyp which formed it, when the latter is in a somewhat contracted condition, and fills the whole coelenteron of its parent.

What stimulus causes the extrusion of the planulae in nature we do not know, but the collection of branches, or the changing of the water in which branches already collected have been standing, seem to act as stimuli for their extrusion. Both of these stimuli are of the nature of *disturbances*; it is conceivable that the natural stimulus is the current set up in the moat during certain phases of the ebb and flow of the tide, or the change of temperature which may accompany it.

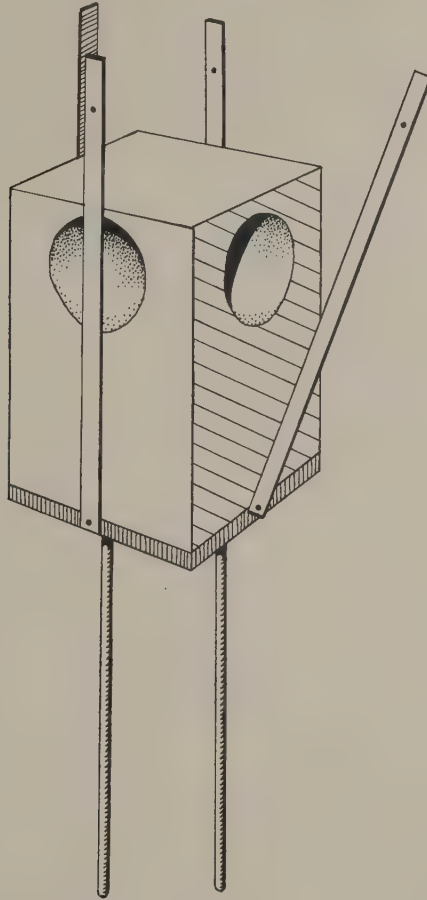
B. THE METHOD OF REARING.

All the young Pocilloporae were reared in finger-bowls, to the inner surface of which they were allowed to attach themselves.* This method was found very convenient, because the bowls were easily handled, and could be placed under a binocular microscope of the type with a long arm, when one wished to study the young corals. After settlement of the planulae had taken place, the bowls were at first submerged in a tank through which sea-water was made to circulate; but later on it was found preferable to plant them out in the sea. The date of birth of the planulae was written on the bowl with a diamond, so that no confusion could take place.

At first the bowls were kept in tanks provided with an arrangement whereby sea-water was allowed to drip into the tank for a certain period of each 24 hours, the excess being carried away through an automatic overflow, so arranged that it removed water from the bottom of the tank. It was not feasible to keep the circulation going throughout

* In some cases young settled colonies showed a tendency to fall off the smooth glass surface of the bowl. It was attempted to correct this by converting the inner surface of a number of bowls into ground-glass, by rubbing it hard with sand, emery powder, etc. This was kindly done for me by Dr. and Mrs. P. D. F. Murray.

the 24 hours, but this did not appear to interfere seriously with the result. Another method tried was the one worked out by Yonge in the case of his experimental corals: here the water was allowed to well up from the *bottom* of the vessel rather rapidly, causing an overflow at the top, twice during the 24 hours. This method is probably preferable to the first, as giving a more adequate water-change. Whichever method is used, the circulating sea-water should be filtered; otherwise the fine sediment which falls out of

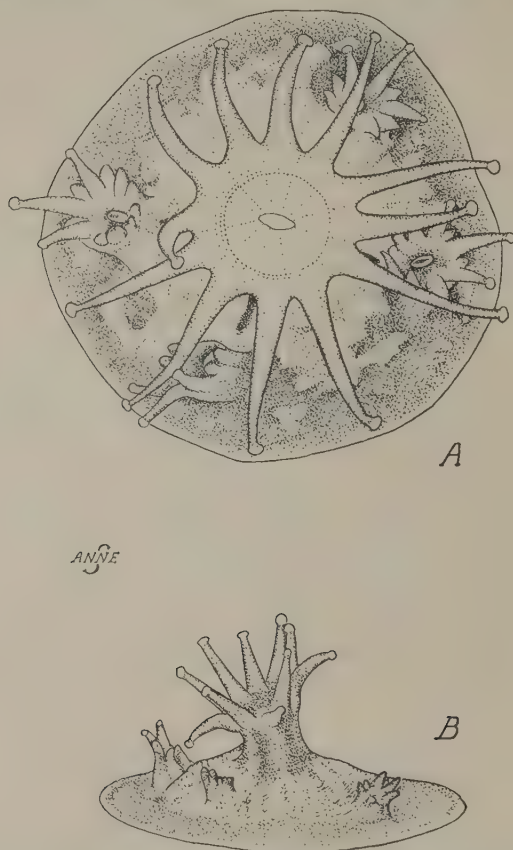


TEXT-FIG. 2.—Diagram to illustrate the structure of the "clock-towers" used for rearing planulae (for description, see text).

suspension becomes too great in amount, and makes it necessary to clean the bowls very often. Both sediment and too frequent cleaning are harmful to the delicate corals.

Later on, however, it was found that it is much better to keep the young corals in the sea; and once this had been discovered, they were placed there as soon as settlement had taken place. This was effected as follows: A number of solid tower-like blocks of concrete were constructed, each being about 14 inches high, and 8×10 inches in transverse section (Text-fig. 2). They were made in a wooden mould with detachable parts, and before the concrete was poured into the mould, four finger-bowls were so arranged inside the mould that, when the cement had set and they could be removed,

each one left a concavity which fitted it exactly, in the cement. The block therefore had the appearance of a small clock-tower with four hollow faces. It also had two long "legs"—two lengths of iron rod about half an inch in diameter and about 2 feet long. Some 6 inches of each rod was inset into the concrete, having been introduced at the time of the

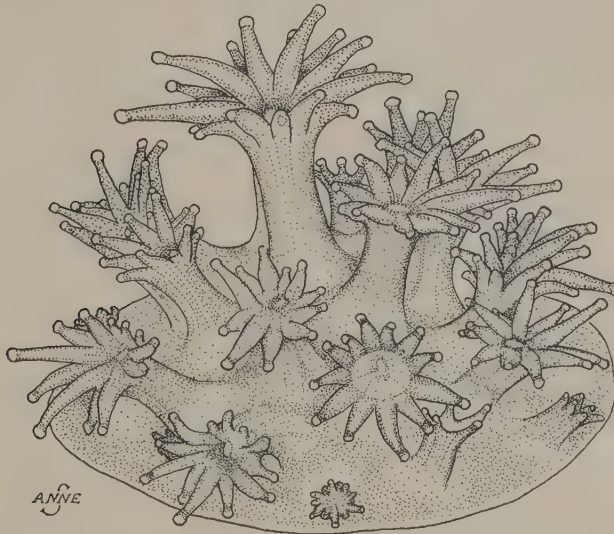


TEXT-FIG. 3.—Young reared colonies of *Pocillopora bulbosa*. A. Colony about 2 weeks 5 days old (counting from date of extrusion of the planula), born on or about 15.xii.28; viewed from above. The colony consists of a single primary polyp and 4 buds. The pale irregular area round the primary polyp represents the thickened part of its skeleton, as seen through the living tissue. The skeletons of the buds have begun to form, and have modified the shape of the thickened part of the skeleton of the primary polyp. B. Colony about 2 weeks 6 days old, born on or about 14.xii.28; viewed from the side. This colony has one primary polyp and three buds, and is slightly less advanced than A. Note the central mound caused by the thickening of the skeleton in this region, and the flat peripheral area. Fig. A, $\times 20$; fig. B, $\times 16$.

making of the block; the remaining 18 inches projected from the bottom of the block. These towers were planted out in the sea, some in the western moat and others in the anchorage, in pools which would retain enough water to cover them at all states of the tide. They were kept in place by the two legs, which were driven into the reef, a hole having previously been made for each with a large crowbar. In each of the four cavities

in the block a finger-bowl was placed. It was prevented from falling out of the hollow by a wooden lath passing vertically across its mouth, up the middle of the side of the block. The four laths were attached, each by a single nail, to a square of thick wood which lay underneath the block, and which was perforated by two holes through which the "legs" passed. This meant that each lath would swivel on its nail, and could be pushed aside when one wished to remove the bowl which it guarded. Between the inspections of the bowls, the four laths were tied together with string or wire passing through holes in their upper ends; these upper ends projected above the top of the block.

To anyone who may try this method in the future, the warning should be given that before the cement is poured into the mould, round the finger-bowls, each finger-bowl should be coated as smoothly as possible with thoroughly greased newspaper, and two pieces of string should be placed round the back of it, with the ends projecting, in order



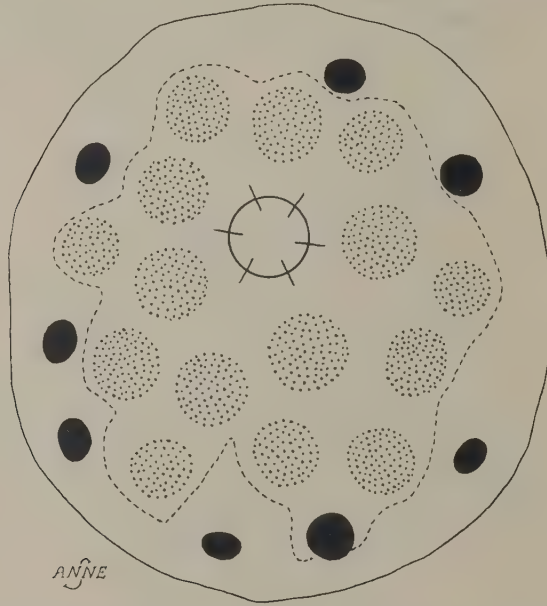
TEXT-FIG. 4.—Side view of the most advanced colony of *Pocillopora bulbosa* reared from a single planula in a finger-bowl. A plan of this colony is reproduced in Text-fig. 5. The planula was born on 14.xii.28, and the drawing made 10 weeks and 5 days after its extrusion. The skeleton does not show at all here, as the coenosarc is raised well above it. $\times 17$.

to facilitate pulling it out afterwards. Even with these precautions it may have to be extracted by breaking it. Further, the "clock-tower" must soak in the sea for some time before use, so that the concrete may be "cured"; otherwise the substances which dissolve out of it may affect the young corals. Three weeks is a safe period for the curing process, but probably somewhat less is actually sufficient.

This method of rearing has several advantages. First of all it enables the young corals to catch plankton for themselves, and overcomes the difficult problem of feeding them artificially. Secondly, it exposes them to approximately natural conditions, and they respond to this by more rapid and normal growth. Thirdly, they require under these conditions very little attention, and need only be visited periodically, so that the bowls may be gently rinsed to prevent too great an accumulation of fine sediment. The bowls are, of course, placed on one side in the tower to prevent the accumulation of too

much sediment—if they were fixed right way up the corals would be smothered by collecting sediment in a short time. It is also important that the bowl should be near the top of the tower—*i. e.* raised some inches above the sand of the pool—otherwise the danger from moving sand and accumulating sediment would be too great. The presence of the lath across the mouth of each bowl did not appear to interfere with the circulation nor to prevent the entry of an adequate amount of food and light. The method, at any rate, proved very successful.

Before the corals were placed in the sea they were fed as follows: When very young they were given small amounts of a culture of protozoa made by keeping some leaves of



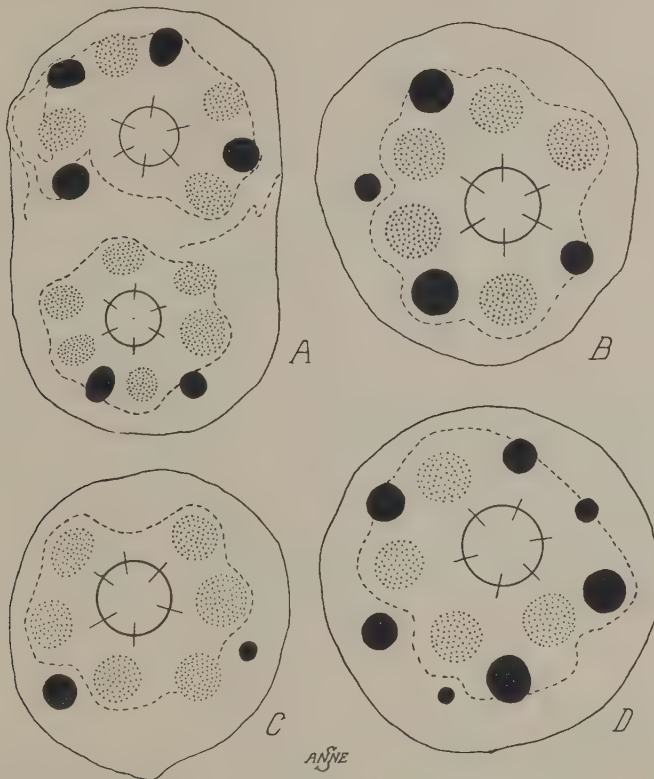
TEXT-FIG. 5.—Plan of the colony represented in Text-fig. 4, drawn 10 weeks and 6 days after extrusion of the planula. The primary polyp is represented by a circle, the six rays indicating the positions of the principal septa. The older buds, of which there are 15, are stippled; the younger ones, 8 in number, are represented in black. The dotted line indicates approximately the edge of the thickened central part of the skeleton. $\times 17$.

Thalassia and a little organic detritus in a separate finger-bowl. The *Thalassia* leaves prevent excessive decay in such a culture, but permit the life of protozoa. Later on, the corals were given freshly-caught plankton from which the larger organisms had been filtered out. How far the corals benefited from this feeding it is impossible to say, but at least they continued to grow. I think, however, they would not continue healthy beyond a certain point unless kept in the sea; moreover, the fall of sediment, even from filtered water, in an aquarium tank, is of a sticky and insidious nature, and not easily removed without damage to the corals. It is clear, both from the tank-rearing and the outdoor-rearing that fine sediment is a serious enemy to young corals.

The keeping of planulae *before* they have settled is more troublesome than afterwards. It is essential to change their water every day, and this can be done by running off the water

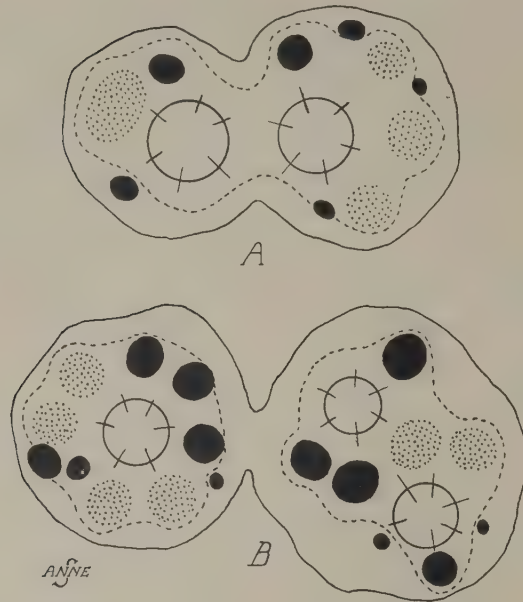
through a glass tube covered at its submerged end by a flattened bag of bolting-silk, to the surface of which the planulae adhere. This is not, however, a very safe method, and may result in fatalities. A better way is to remove each planula to clean water with a pipette; but this is very tedious.

A large amount of material was preserved for detailed study later. Some of the attached polyps or colonies were fixed in neutral formalin (so preserving both skeleton



TEXT-FIG. 6.—Plans of young reared colonies of *Pocillopora bulbosa*, illustrating the arrangement and order of appearance of the early buds. The conventions adopted are as in Text-fig. 5. A. Colony 7 weeks 6 days old, born 15.xii.28; formed by fusion of two primary polyps, and subsequent budding. The colonies figured in B, C, and D, were each formed by budding from a single primary polyp, and were born on same date as A. C and D were the same age as A; B was one day older, at the time of drawing. Note that the primary circle of buds consists of 4, 5, or 6 buds. Magnifications similar to those of Text-fig. 7.

and soft parts), others in Bouin's fluid, which, of course, decalcifies them; in either case they were transferred for storage to 70% alcohol. The fixation, especially by means of Bouin, has proved to be excellent. Free-swimming planulae were fixed either in Bouin or Champy. Skeletons were prepared by gently pouring a hot solution of KOH (10%) on to the young corals; this removed the tissue easily in most cases (sometimes it had to be done more than once), and did no damage to the delicate skeletons, which were afterwards well washed.



TEXT-FIG. 7.—Further plans of young reared colonies of *Pocillopora bulbosa*: conventions as in figs. 5 and 6. A. Colony formed from fusion of two primary polyps, and subsequent budding. A case in which two semicircles of buds have been formed, on the sides of the primary polyps which are turned away from each other, no buds having appeared between the two. Age of colony about 7 weeks, extrusion of planulae on or about 15.xii.28. B. Colony formed by fusion of 3 primary polyps, and subsequent budding. In the right-hand half of the colony budding is irregular, and buds have appeared between the two primary polyps. Age of colony about 6 weeks 4 days, extrusion of planulae on or about 15.xii.28. A, $\times 16$; B, $\times 12$.

C. THE DEVELOPMENT OF THE COLONY AFTER THE ATTACHMENT OF THE LARVA.

The fixation of the planula sometimes takes place within 24 hours after its extrusion; in other cases it does not occur for two or three days, or for a week or more. How long the free-swimming period lasts, in the sea, I cannot tell, but I suspect that it is short. Planulae in captivity tend to settle within a few days of extrusion, or else appear disinclined to do so at all; such as had failed to do so after about ten days in captivity were usually preserved, as they no longer seemed normal.

This disinclination to settle may have been due to premature extrusion of a proportion of the planulae, as a result of the disturbance caused to the parent branches by collecting them; had the branches been left undisturbed in the sea, such planulae might well have remained longer in the coelenteron of the parent polyp. This perhaps accounts for part of the number which fail to settle; but against it must be put the consideration that many of the planulae which do not settle appear to be stout and well-developed individuals. This suggests rather that unless they settle fairly soon in captivity, their condition becomes in some way pathological, although they do not appear actually unhealthy. Before a planula settles definitely, it may attach itself temporarily to the substratum, and become dome-shaped; but will afterwards swim away again, and resume its ordinary form.

I suspect that the planulae, during their brief free life in the sea, often remain near the bottom and are not carried far afield. A tow-netting was taken by S. M. Marshall and myself on a day when *Pocillopora* was known to be fertile (and when planulae could be obtained by picking branches), right round the moat, and only a foot or so above the coral. Not a single planula was captured. This must mean either that any planulae recently extruded had been swept away, or that they were actually among the coral near the bottom; or that few had been extruded although the parent colonies were fertile. In the regular tow-nettings taken by Russell and Colman coral planulae were of notably rare occurrence. They were not found in any of the hauls taken over the reef-flat; and at the plankton station three miles from the reef they were taken only on three occasions



TEXT-FIG. 8.—A young living colony (reared) of *Pocillopora bulbosa*, viewed from above. The colony was formed by fusion of 8 primary polyps, and subsequent budding. The 8 planulae were extruded on or about 15. xii. 28, and the colony was about two weeks old at the time of drawing. One of the primary polyps is contracted. Nine buds have appeared. $\times 12$.

(14th, 19th and 27th December, 1928), and only once (14th December) in quantity. A certain number of planulae, probably belonging to *Acropora*, were obtained by S. M. Marshall from tow-nettings in the anchorage on 24th, 26th and 27th December, 1928.

When the planula definitely settles down and becomes firmly attached it becomes apparently much larger, because it spreads out flat and becomes thin and coin-like, an attenuated disc with a slight mound in the centre, and with a diameter of 1.7–1.8 mm. or more. It begins to secrete skeleton almost at once; so rapidly, indeed, that one rarely catches a polyp which has settled but which has no skeleton. The appearance of a normal polyp shortly after settlement is illustrated in Plate I, fig. 2. This shows the disc-like form, the central mound bearing the small mouth with its narrow pale-green lip; no tentacles have yet developed, but the skeleton is well formed; the thin basal plate is clearly visible round the edge of the polyp, where it projects beyond the tissues of the latter,



TEXT-FIG. 9.—A young reared colony of *Pocillopora bulbosa*, viewed from one side. It consists of 9 primary polyps, which have fused, and a number of buds, of which 12 are visible. Age of colony about 2 weeks 4 days, planulae extruded on or about 14. xli. 28. $\times 13$.

or is covered by a very thin membrane only; there are 24 septa (in three alternating cycles), visible as white rays through the outer part of the polyp's tissues; and the body of the polyp has 12 radial cream-coloured stripes, 6 principal and 6 subsidiary.

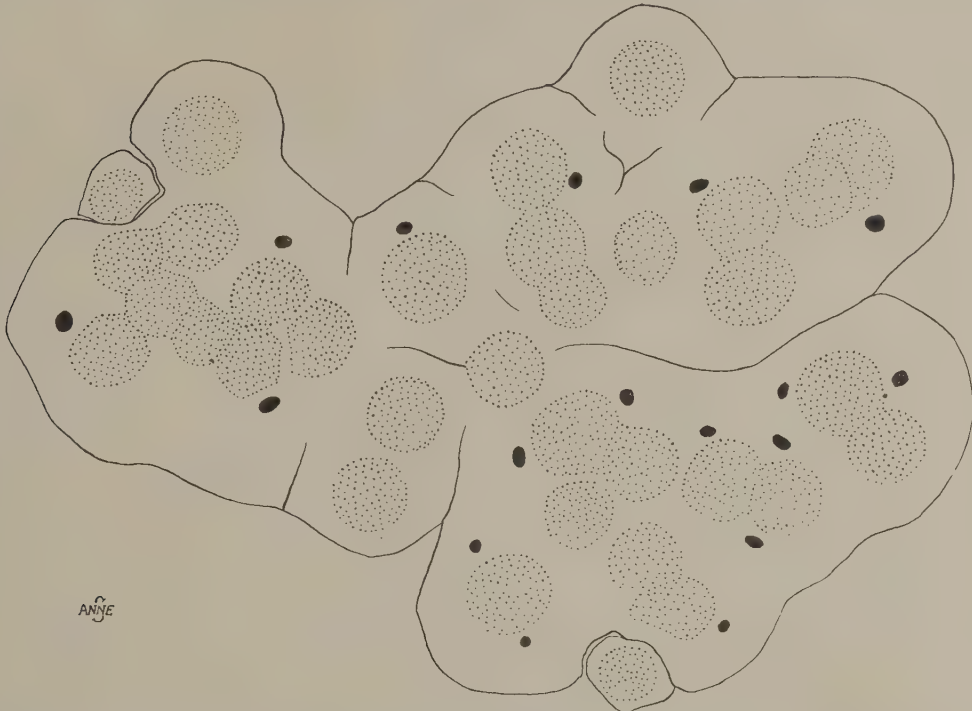
It happens fairly often that for some reason a planula which has become more or less flattened fails to settle; it may become entangled in the surface-film, or may for some other reason fail to attach itself. But, in spite of this, it may begin to form a skeleton, which, as a result of the non-attachment of the larva, has not the normal form, and may be considerably distorted. Once this skeleton has started, in the majority of cases the larva has no longer any chance of attaching itself, and is bound to die sooner or later. This state of affairs suggests that the stimulus to form a skeleton is an internal one, which may come into action at a given time, even in the absence of the additional stimulus which, in a normal case, is supplied by contact with the substratum. Presumably, in a normal case, both stimuli may be effective. These unattached polyps may also develop tentacles.

The tentacles of the normal polyp begin to grow out as small papillae very soon after settlement; in some cases they are discernible within 24 hours of fixation, and in a few days they attain full size. They appear approximately simultaneously, and normally grow at about the same rate; so that the polyp, when fully formed, has 12 tentacles, arranged in two cycles, 6 exocoelic and 6 endocoelic, the endocoelic ones being a little the longer. If any other unevenness in the lengths of the tentacles appears, it follows no systematic plan. This is in sharp contrast to the development of the tentacles in buds, which, as will be seen later, takes place in a different manner.

Before describing the development of the colony, we must notice a curious feature which has already been described by Boschma for *Meandra areolata*, and by other authors for other corals. Under the conditions of rearing which prevail in a finger-bowl, a rather large number of settled polyps may be living together in a small space; this is accentuated by the fact that they have a tendency to settle particularly thickly just beneath the water-line, and also round the groove where the sides and bottom of the bowl meet. As a consequence, if two or more polyps settle very close to one another, they soon grow, increase their area, and come into contact with one another. As

soon as this happens, they fuse; and the fusion becomes so complete, both as regards flesh and skeleton, that the independent organisms become one. Therefore, colonies are formed at this stage, not by budding or by fission, but by the fusion of independent primary polyps. A number of these fusions are illustrated in the accompanying plates and text-figures, the details of each example being explained in connection with its figure.

After a period* during which the primary polyp or polyps simply grow and add to their skeletons, budding begins. This will be described first in the typical case, *i. e.* in the case of a single polyp which has not fused with any others, and which can



TEXT-FIG. 10.—Plan of a young reared colony of *Pocillopora bulbosa*, formed by the fusion of 32 primary polyps and the subsequent production of 17 buds. Two other primary polyps have nearly fused with the main colony. All the buds were in a very young condition at the time of drawing. Age of colony about 2 weeks 6 days, extrusion of planulae on or about 15. xii. 28. $\times 9$.

therefore develop unfettered. The story briefly is this: there appears first, round the base of the primary polyp, a single circle of buds (which do not usually appear simultaneously); after these have undergone a certain amount of development a second circle appears, alternating more or less regularly with the first, and placed further out from the primary polyp; and so on. The development of these successive circles is not, however, perfectly regular, and tends to become less so with age. The first circle may consist of

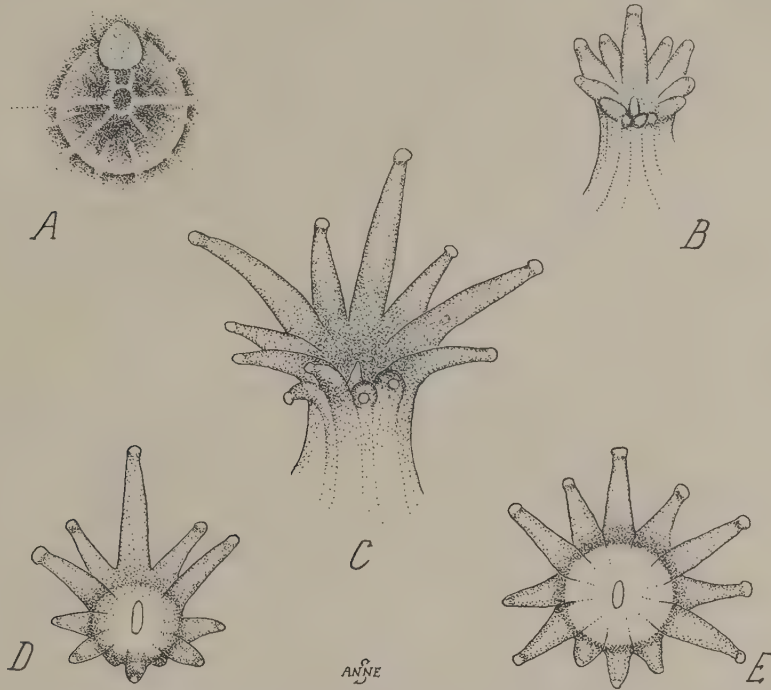
* I have not given details as to the exact times after the extrusion of the planulae at which the various stages are reached, because these times vary too much, according to circumstances, to have much significance in a summary statement. But the age of each stage figured, wherever known, is stated in the explanations of the plates and text-figures, so amplifying the text. This point will be further elaborated later.

6 buds, more or less evenly spaced out ; but almost equally often it consists of 4 or 5, and sometimes of 3 or of 7 ; these buds may be fairly evenly or distinctly irregularly placed. As growth proceeds there is a tendency for the number of buds on one side of the colony to become greater than on the other, so that it loses its original symmetry. During the early stages, therefore, the colony grows out laterally, retaining its disc-like form, but increasing its area. At the same time, while this budding has been going on, the skeleton has been increasing in thickness in its central parts ; from a very early stage the central region has assumed the shape of a low mound. The thickening affects, at first, only the calyx of the primary polyp but soon spreads further afield. (This thickening-up of the skeleton tends to take place less markedly in colonies reared in finger-bowls than in those which have developed naturally in the wild.)

After a time the colony has reached the condition illustrated in Plate III, fig. 4, in which it forms a thickened, irregular disc with numerous corallites derived by budding from a single parent ; it shows as yet no branched structure. The figures on Plate VI illustrate the transition from this condition to that of the adult colony. In fig. 1 the colony has become conical ; in fig. 2 a definite upward-growing branch has appeared ; in fig. 3 the branch has subdivided. In figs. 4 and 5 several branches have grown out independently from the basal expansion ; and in the remaining figures intermediate stages between a colony with a single branch or with a few simple branches, and the adult many-branched condition, are illustrated. The figures on this plate were obtained as follows : The most advanced colony reared *in a finger-bowl* is that illustrated in Text-figs. 4 and 5, and in Plate III, fig. 1. The stages shown in Plate VI, figs. 1-3, were obtained by planting out logs of wood in the Madreporite moat ; and a number of other similar ones were procured by planting out other materials (pieces of clean beach sandstone, clean dried clam-shells, pieces of drain-pipe, etc.) in various positions on the reef. These materials were fastened down so that they could not move, and a number of planulae of *Pocillopora* and other corals settled upon them during the course of the year. The exact age of the colonies so obtained is, of course, not known ; but since the dates of planting out each deposit of materials and those of the collection of each young colony are known, any such colony is younger than the interval of time between the setting out of the materials and the collection of the young coral. The remaining figures on Plate VI are from a series of colonies collected on the reef, but are of unknown age. The outline of development just given refers, of course, to typical cases ; a number of aberrant or exceptional examples are, as always, to be found, but these will be dealt with in Part II.

So much for the course of events in a colony founded by a single polyp. In the case of colonies formed by fusion, the early development is somewhat modified, but after a certain point the procedure must be much as in the normal case. The early modification is due mainly to the fact that in a compound colony, unless the calices of the primary polyps are sufficiently distant one from another on the common basal plate, a ring of buds cannot develop freely round each, and the production of buds becomes to a greater or lesser degree irregular. If the calices of two or more fused polyps lie very close together (actually in contact), buds do not, in any case I have seen, develop between them, but only round the sides which are turned away from each other, or in the angles between them ; *i. e.* the fused polyps form a nucleus about which buds will develop. If however, there is any space between the primary polyps, even quite a narrow one, buds may develop between them ; but this does not always happen, since sometimes, even

when the interval is considerable, no buds arise from it during the early stages, but develop in semicircles round the sides of the primary polyps which do not face each other. This applies only to early stages, however; as soon as the first branch begins to appear, new buds develop, in the growing region, between very close-set calices.

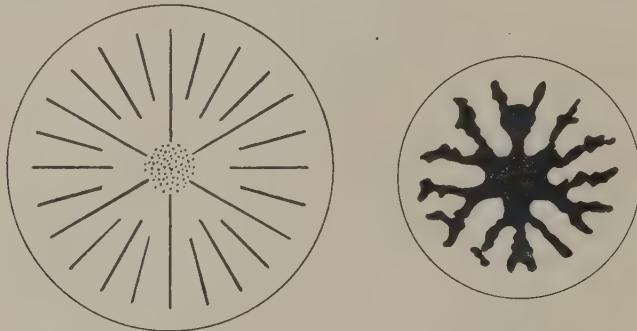


TEXT-FIG. 11.—A series of buds of *Pocillopora bulbosa*, much enlarged (A being more magnified than the others), to illustrate the symmetry of the buds and the development of their tentacles. All the figures are similarly oriented—*i. e.* the lower side of each figure represents the side of the bud which faces the primary polyp or the centre of the colony; vertical lines drawn through the centre of each figure would therefore represent approximately radii of the colony. A, very young bud with one short directive-tentacle only; the mouth is formed, and the 6 couples of mesenteries are visible because of the transparency of the tissues. The other figures illustrate the bilateral appearance of the tentacles, in couples symmetrical about the directive axis; the dominance, maintained for some time, of the first directive-tentacle to appear; and the shortness of the tentacles on the side of the bud which faces the centre of the colony.

Lastly, the development of the buds themselves may be considered; it is illustrated in Text-fig. 11. The bud when first seen consists of a small mound, which rapidly attains the stage illustrated in fig. A, in which not only the mouth, but also the mesenteries and a single short tentacle are visible. This tentacle is always the first to appear, and it is the directive tentacle farthest away from the primary polyp of the colony. In other words, the bud, at the present stage of its life, is bilaterally symmetrical about its directive axis, and its directive axis coincides with a radius of the whole colony.* This markedly bilateral

* This applies strictly, of course, only in the case of radially symmetrical colonies, *i. e.* those derived from a single planula, and is subject to the reservation that the coincidence between radius of colony and directive axis of bud is sometimes approximate rather than exact. In colonies formed by fusion, the buds arise with as nearly the typical orientation as circumstances permit.

phase is maintained for a long time. The remaining figures, B-E, show how the rest of the 12 tentacles develop—in couples, of approximately the same length in each couple, one member of each couple being placed on either side of the directive axis of the bud, *i. e.* on either side of a radius of the colony. The long axis of the mouth corresponds, of course, with the directive axis; and the oral disc tends to be oval, the longer axis at right angles to the directive axis. It is further apparent from these and some of the other figures, that the tentacles on the side of the bud *nearest the primary polyp* are shorter than the rest, and this condition also persists for a long time. It has the effect, in the whole colony, of making an even web of tentacles (Text-fig. 4), covering the whole surface, when the polyps are expanded; the short inner tentacles of the buds do not interfere either with the long outer tentacles of any buds more centrally placed than themselves, nor with those of the primary polyp; and between the buds and the primary polyp much of the available area is covered.



TEXT-FIG. 12.—Diagrammatic representation of the skeletons of young polyps of *Pocillopora bulbosa* (left-hand figure) and *Porites haddoni*. Both figures are to the same scale ($\times 20$). The *Pocillopora* was drawn from a skeleton about 5 weeks 6 days old, the planula extruded on or about 14.xii.28. The *Porites* was from a specimen 7 days old (planula extruded 7.ii.29). The polyp belonging to this skeleton had its tentacles at the stage represented in Text-fig. 13, B. The finer detail is not represented in this figure, since the skeleton was drawn as seen through the flesh of the polyp. (The specimen of *Pocillopora* used for this diagram was unusually backward in development for its age.)

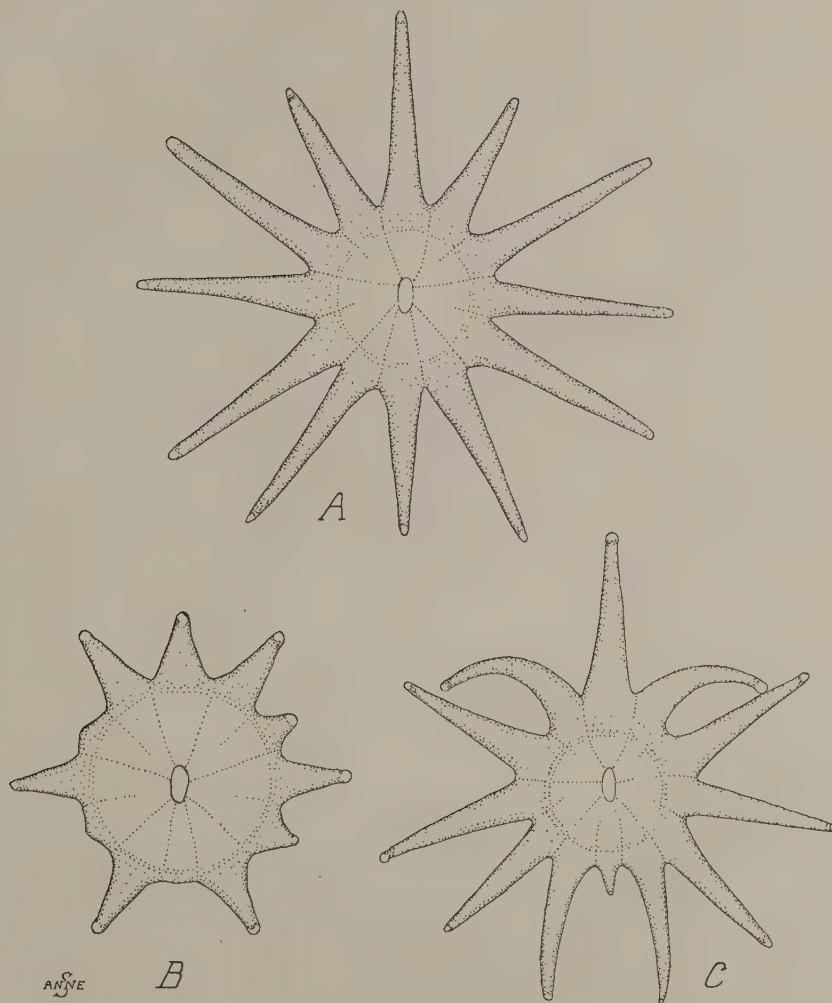
D. THE PROGRESSIVE MODIFICATION OF THE SKELETON.

To what has already been said it is necessary to add that the outline of skeletal development is as follows: At first the septa are independent ridges on the basal plate (Text-fig. 12, Plate II, figs. 1 and 6); later on they fuse and form a raised corona or calyx (Plate II, figs. 2-4). In the early stages of calyx-formation the six principal septa meet or nearly meet (in a typical case) a central columella. In cases which appear to be atypical, there may be a ring-like skeletal structure in the centre, instead of a columella; and other variations. Both the calyx and the plate become prickly. The skeleton of a primary bud has at first six conspicuous primary septa and a columella. As development proceeds, the coenenchyme between the corallites becomes thickened (Plate III, figs. 1 and 4). When the colony begins to form branches, the shape of the newly-formed corallites is different from that of the earlier ones (Plate VI, figs. 1-5); and as a branch grows upwards, the proximal calices became different from the distal ones. The details will be described in Part II.

III. *PORITES HADDONI*.

A. THE EXTRUSION OF PLANULAE.

The species of *Porites* which provided the planulae for rearing was common in the Low Isles moats. It was one of the massive forms, without branches or actual lobes, the



TEXT-FIG. 13.—The arrangement of tentacles in primary polyps of *Porites haddoni*. B, in a polyp 7 days old (planula extruded 7.ii.29); here only 11 of the 12 tentacles have appeared, 4 are still very short, and the bilateral arrangement is very marked. The mesenteries are indicated by dotted lines. The central ray of the trident in the skeleton (Text-fig. 12) corresponds to the directive endocoel which has not yet developed a tentacle. C, in a polyp 7 weeks 4 days old (planula extruded 7.ii.29); here the tentacles are longer, but the bilateral arrangement is still marked; the curious curvature of the tentacles shown is habitual in some polyps. A, in a polyp of the same age as C, born the same day and reared in the same bowl, but in which the tentacles have attained a more radially symmetrical condition; traces of bilateral symmetry still remain. Fig. B is magnified 32 diameters, the other figures considerably less.

surface being at most irregular or nodulated. The majority of the planulae were obtained from young colonies, since these are easier to collect than large ones, besides which they seemed more ready to extrude planulae. The colour of the colonies varied from cream or pale fawn to yellowish or purplish. I speak of the coral in question as *Porites haddoni*; but it is not impossible that more than one species provided us with planulae. The identification of *Porites* down to a species, is probably impossible in the field; and in any case there is no real certainty as to what characteristics constitute specific limits in the genus, the matter being still within the realm of personal opinion. We can only say that our specimens were derived from a common habitat; that they may well have belonged to a single species; and that the development of their planulae presents a coherent story with no suggestion of specific differences in ontogeny.

The first planulae observed from *Porites* were found by Yonge in an aquarium tank on 26th January, 1929. From that time onwards *Porites* were brought in from the reef every few days, until 22nd July. The production of planulae went on all the time. In this case the breeding appeared to be continuous, with no suggestion of periodicity, but the number produced fell off greatly in June and July. The details of this spawning, as in the case of *Pocillopora*, will be recorded in the report on breeding of reef animals.

The method of obtaining the planulae was the same as in *Pocillopora*, by bringing in colonies in a bucket. The rearing also followed the same plan, but that in one case some planulae settled in a small tank, and this was planted out in the sea, on end, in a special cement tower of its own. In the case of *Porites* the finger-bowls were all put out in the sea as soon as the planulae had settled, none of the latter being reared under aquarium conditions. The planulae of *Porites* are smaller than average planulae of *Pocillopora*, and paler in colour; otherwise they call for no further comment in this part of the paper.

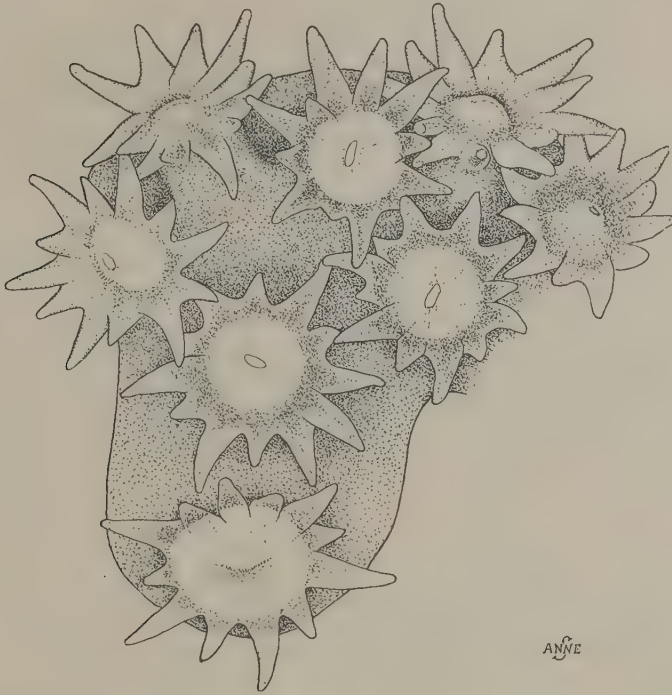
B. THE DEVELOPMENT OF THE COLONY AFTER THE ATTACHMENT OF THE LARVA.

The general outline of the early stages is the same here as in *Pocillopora*, with certain sharp differences of detail. I can say nothing about the way in which the successive buds arise in this case, because although my colonies produced a large number of buds, they grew rather slowly, and had not time to produce more than an initial number while they were under observation. Moreover, I had a considerable proportion of fusion-colonies, and fusion always complicates the arrangement of buds.

The skeleton of a young *Porites* polyp is very different from that of a young *Pocillopora*, consisting, apart from the basal plate, of a series of irregular radial elements, which from an early age have the bilateral arrangement shown in Text-fig. 12. When fusion takes place, as it does very readily and on a large scale, the skeletons (but not the soft parts) of individual polyps may lose their identity altogether, and become lost in a confused tangle of lace-like trabeculae (Plate IV, fig. 1).

The development of the tentacles in the settled larva of *Porites* is also unlike that of *Pocillopora*. Instead of growing out approximately evenly, they have a strongly-marked bilateral arrangement from the very beginning (Text-fig. 13, B), and even when they

become long and more equal in length, traces of the bilateral condition usually still persist. The number of tentacles is normally 12, but sometimes other numbers (10, 18, etc.) occur. Another peculiarity is this—that in a fusion-colony consisting of a number of primary individuals, those round the edge tend to grow longer tentacles on the side which is turned away from the middle of the colony than on the side turned towards the middle. This means that they grow longer tentacles on the side where these can stretch out freely without coming into contact with the tentacles of adjacent polyps; there is no constant relation



TEXT-FIG. 14.—Part of a colony of *Pocillopora haddoni* formed by the fusion of 19 primary polyps, of which 8 are shown. No budding has yet taken place. Age of colony 7 days; planulae extruded 7.ii.29. $\times 20$.

here between the lengths of the tentacles and the directive axis. A colony of this description, therefore, repeats to some extent the state of affairs found in a colony such as that illustrated in Text-fig. 4; but in this case it is not *buds* which have long outer tentacles, but primary polyps. Inequality of the tentacles of primary polyps, in this sense, is sometimes seen in *Pocillopora* in a less marked degree.

The development of the buds in *Porites* follows that of the buds of *Pocillopora* very closely—*i. e.* a single directive tentacle appears first, on the side of the bud farthest from the centre of the colony, and the remaining tentacles develop bilaterally about the directive axis of the bud, which coincides more or less closely with a radius of the colony. The tentacles on the side nearest the centre of the colony remain, as before, shorter than the others for some time.



TEXT-FIG. 15.—Part of a colony of *Porites haddoni* formed by the fusion of 19 primary polyps. The tentacles have become longer than in Text-fig. 14, and the tendency of the marginal polyps to develop long tentacles on the side of the polyp turned away from the centre of the colony is clearly illustrated. Two buds (visible as knobs without tentacles) are present. Age of colony 7 weeks 6 days; planulae extruded 7.ii.29. Magnification somewhat less than that of Text-fig. 14.

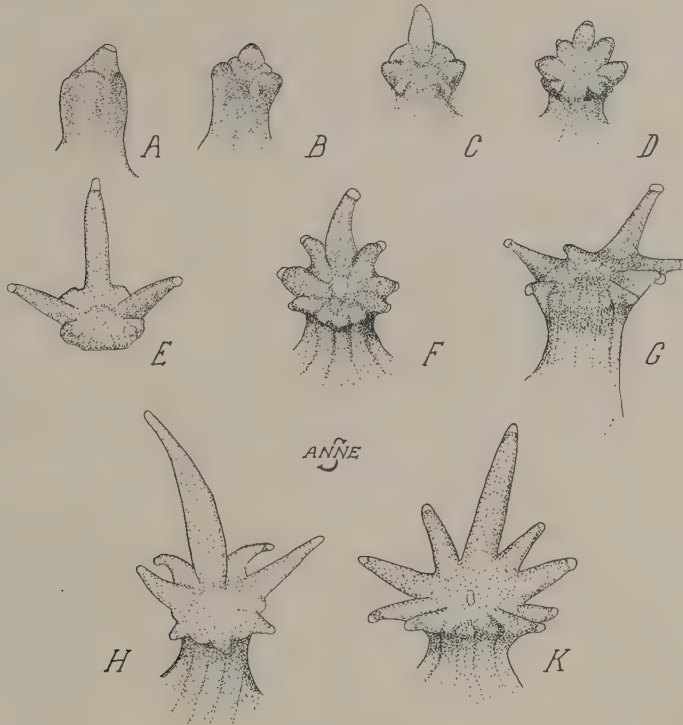
IV. THE RESPONSE OF YOUNG COLONIES TO SEDIMENTATION.

In the photographs of young skeletons reproduced in the plates, both in those of *Pocillopora* and in those of *Porites*, it will be noticed that certain of the young colonies have a raised rim, sometimes broad and incurved, either round the margin of the basal plate, or in some more central position. These rims are, I believe, a response to accumulations of fine sediment, matted together by a microscopic growth of algae, which frequently form round the edges or even upon the surfaces of young corals. That the rims are a response to certain conditions in the environment, and are not a necessary part of the corallum, constituting a specific characteristic, is suggested by the following considerations:

1. In both *Pocillopora* and *Porites* the rims in question are present only in certain individuals. That the rimless condition is normal and healthy in *Pocillopora* I feel certain. In *Porites* a well-developed rim is very often present, but this coral has a very small polyp,

more easily subdued than that of *Pocillopora*, and may well need to react more strongly. When working on the living material, I gained the impression very distinctly that the absence of a rim was the more normal and healthy condition, and that the rim was put up to keep off deleterious substances from damaging the delicate flesh at the edge of the colony.

2. The mode of occurrence of the rims, when they are present, is erratic. In fusion-colonies of *Porites* (Plate IV, fig. 1; Plate V, figs. 5-9, 11) these rims may or may not occur between the fused corallites. This should not be the case if the presence of the rims is a



TEXT-FIG. 16.—A series of buds of *Porites haddoni*, illustrating the form and orientation of the bud, the predominance during the early stages of the first directive-tentacle to appear, and the bilateral appearance of the other tentacles. The figures are oriented as in Text-fig. 11, and are much enlarged.

specific feature. Moreover, a rim is often present in one part of the circumference of a colony, absent in another part. Again, there may be two rims (complete or incomplete), one inside the other; or a single rim at the edge, or a little way in from the edge.

3. In a number of colonies the rim does not occur either at or near the edge, as it should if it were a regular morphological feature. A particularly good example of this is shown in Plate III, fig. 6, which represents a colony of *Pocillopora* with an irregular rim surrounding the white central part of the colony only. In this colony, at the time when it was fixed, the central part (clean and white in the skeleton) was alive and healthy; but the peripheral part, outside the rim, was dead, and was matted with the algae and sediment which had killed it. Another such colony is shown in fig. 7 of the same plate, and here the living

parts of the colony, at the time of fixation, were limited to two small areas including the two primary polyps—these areas are just distinguishable in the figure, each with its surrounding ridge. Such instances are plentiful, and the protective ridges thus formed often cut right across the corallite of a dead or half-dead polyp (as in fig. 7, on the right).

REFERENCES.

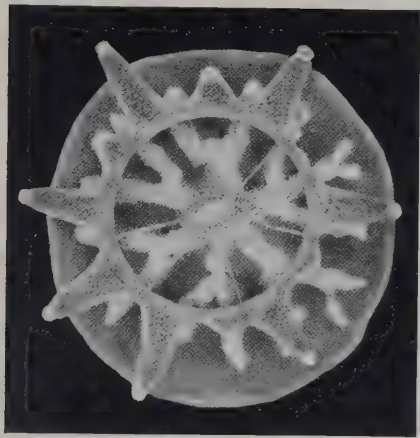
(For further references see Boschma, 1929; Matthai, 1926; Duerden, 1902.)

- BOSCHMA, H. 1923. Experimental Budding in *Fungia fungites*. Proc. Kon. Ak. Wetensch. XXVI, Amsterdam, p. 88.
- 1929. On the Post-larval Development of the Coral *Maeandra areolata* (L.). Carnegie Inst. Washington, Publication no. 391, Washington, p. 129.
- BOURNE, G. C. 1899. Studies on the Structure and Formation of the Calcareous Skeleton of the Anthozoa. Quart. Journ. Micro. Sci. XLI, London, p. 499.
- DUERDEN, J. E. 1902. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci. VIII, No. 7, Washington, p. 401.
- 1902. Increase of Mesenteries in Madreporaria Beyond the Protocnemic Stage. Ann. Mag. Nat. Hist. ser. 7, X, London, p. 96.
- 1902. The Significance of Budding and Fission. Ann. Mag. Nat. Hist., ser. 7, X, London, p. 382.
- 1903. Fissiparous Gemmation. Ann. Mag. Nat. Hist., ser. 7, XI, London, p. 141.
- 1904. The Coral *Siderastrea radians* and its Post-larval Development. Carnegie Inst. Washington, Publication no. 20, Washington, pp. 130.
- 1905. Recent Results on the Morphology and Development of Coral Polyps. Smithsonian Misc. Coll. XLVII, Washington, p. 93.
- EDMONDSON, C. H. 1928. The Ecology of an Hawaiian Coral Reef. Bernice P. Bishop Museum, Bulletin 45, Honolulu, pp. 64.
- 1929. Growth of Hawaiian Corals. Bernice P. Bishop Museum, Bulletin 58, Honolulu, pp. 38.
- HADDON, A. C. 1892. The Newly Hatched Larva of *Euphyllia*. Sci. Proc. Roy. Dubl. Soc. VII, Dublin, p. 127.
- KOCH, G. VON. 1882. Über die Entwicklung des Kalkskeletes von *Asteroides calycularis* und dessen morphologischer Bedeutung. Mitt. Zool. Stat. Neapel. Bd. III, Leipzig, p. 284.
- 1892. Aggregirte Kolonien von *Balanophyllia verrucaria* Aut. Morph. Jahrb. Bd. XVIII, Leipzig, p. 376.
- 1897. Entwicklung von *Caryophyllia cyathus*. Mitt. Zool. Stat. Neapel, Bd. XII, Berlin, p. 755.
- LACAZE-DUTHIERS, H. DE. 1873. Développement des Coralliaires. Deuxième Mémoire : Actiniaires à Polypier. Arch. Zool. Exp. Gen. t. II, Paris, p. 269.
- 1894. Faune du Golfe du Lion. Evolution du Polypier de *Flabellum anthophyllum*. Arch. Zool. Exp. Gen. (3), t. II, Paris, p. 445.
- 1897. Faune du Golfe du Lion. Coralliaires. Zoanthaires Sclérodermes (Deuxième Mémoire). Arch. Zool. Exp. Gen. (3), t. V, Paris, p. 1.
- MATTHAI, G. 1926. Colony-formation in Astraeid Corals. Phil. Trans. Roy. Soc. ser. B, CCXIV, London, p. 313.
- MAVOR, J. W. 1915. On the Development of the Coral *Agaricia fragilis* Dana. Proc. Amer. Acad. Arts Sci. LI, Boston, p. 485.
- WILSON, H. V. 1888. On the Development of *Manicina areolata*. Journ. Morph. II, Boston, p. 191.

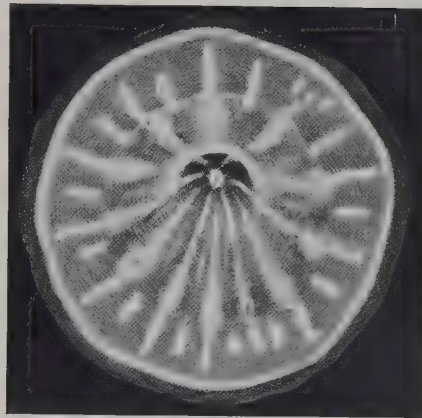
DESCRIPTION OF PLATE I.

(In this and the following plates the magnifications are given exactly or to the nearest whole number ; they are calculated from diameters. The same applies to the text-figures.)

- FIG. 1.—A polyp of *Porites haddoni*, 7 days after the extrusion of the planula, which occurred on 7.ii.29. The tentacles are still in an early stage of formation, and are bilaterally arranged. The skeleton is partially visible through the translucent tissues. $\times 35$.
- FIG. 2.—A very young polyp of *Pocillopora bulbosa*, which had been settled for at least a day. It has not yet developed tentacles, but has a mouth, a basal plate (projecting a little beyond the tissues of the polyp), and 24 septa in three cycles (visible as white radial streaks through the flesh of the peripheral part of the polyp). The central part of the polyp is mound-shaped, and has radial bands of cream-coloured pigment, in two cycles. Drawn 17.xii.28. $\times 23$.
- FIG. 3.—A young colony of *Porites haddoni*, consisting of 4 polyps, of which probably two are primaries and two are buds ; they are shown in a contracted condition. The colony was about 4 weeks old, the planulae being extruded shortly before 5.ii.29. $\times 30$.
- FIG. 4.—A young colony of *Porites haddoni*, formed by the fusion of 3 primary polyps, which are here shown fully expanded, so that the skeleton is completely concealed. The colony was 5 weeks and 2 days old, the planulae being extruded on 7.ii.29. The colony also possessed a small polyp (hidden in the drawing by one of the larger ones) which was probably a bud. $\times 13$.
- FIG. 5.—A young colony of *Pocillopora bulbosa*, viewed from above. The colony consists of a single primary polyp surrounded by 9 buds. The calices of the buds are well formed, and are fused with that of the primary polyp ; the pale spots on the basal plate are skeletal spines showing through the coenosarc ; a crescent of exposed basal plate is visible round the N.E. side of the colony, where the coenosarc has slightly withdrawn. The colony was about 6 weeks 6 days old, the planula having been extruded on or about 15.xii.28. $\times 22$.



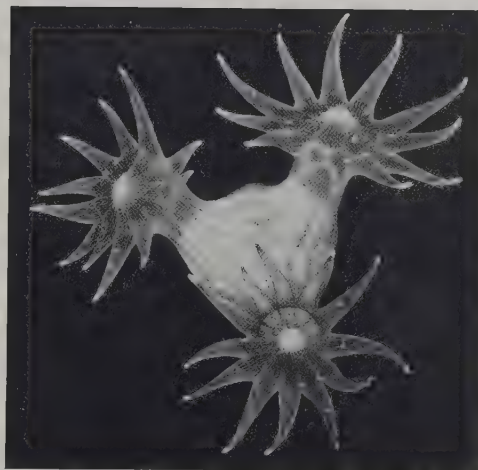
1



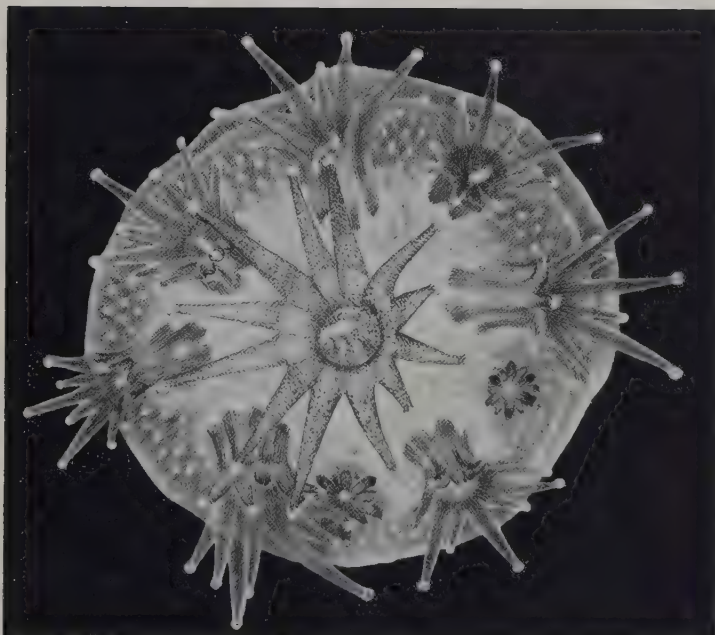
2



3



4



5

DESCRIPTION OF PLATE II.

Pocillopora bulbosa.

- FIG. 1.—Skeleton of a primary polyp about 6 weeks 5 days old (born on or about 14.xii.28), which still has the septa in a distinct condition, not yet fused into a ring. There are 24 septa in 3 cycles—6.6.12. The basal plate here is much broken. $\times 12$.
- FIG. 2.—Stage intermediate between those illustrated by figs. 1 and 3. Same age as those shown in figs. 1 and 3. $\times 12$.
- FIG. 3.—A typical corallum at the stage where the septa have fused to form a ring or calyx. Same age as the coralla illustrated in figs. 1 and 2. $\times 12$.
- FIG. 4.—Drawing of a stage comparable to that shown in fig. 3, but showing the detail of the spines and of the margin of the calyx. Age of specimen, about 16 days, born on or about 15.xii.28. $\times 26$.
- FIG. 5.—Fusion of the corallites of two primary polyps at about the stage represented in fig. 2; and of the same age as the one there figured. $\times 12$.
- FIG. 6.—A group of 8 fused corallites, derived from 8 fused polyps. This figure represents part of fig. 7 still further enlarged, and shows more detail. It shows how individual corallites in one and the same colony may be in different stages of formation at the same time, although the planulae giving rise to them were extruded approximately simultaneously. $\times 7.5$.
- FIG. 7.—A typical group of corallites, in the positions which their polyps assumed naturally in a finger-bowl. Some of the corallites are not yet included in the general fusion, but had the group lived longer they would all have united into a single colony. The polyps were killed about 16 days after the extrusion of the planulae (which occurred on or about 15.xii.28). $\times 4.5$.

1

2

3

4

5

6

7

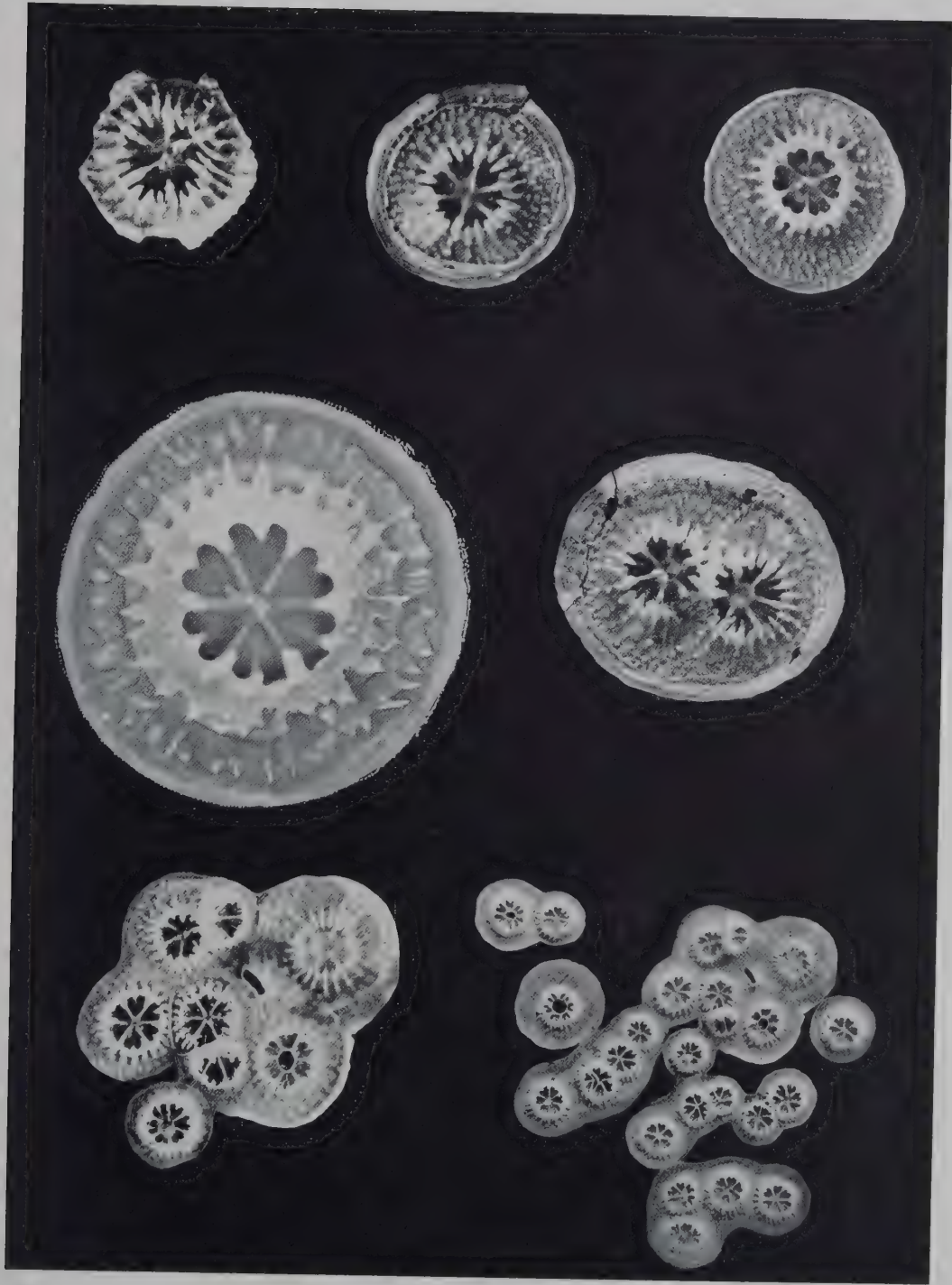


Photo F. Pitlock.
Fig. 4 drawn by Eleanor Dale.

DESCRIPTION OF PLATE III.

Pocillopora bulbosa.

- FIG. 1.—Skeleton of the colony illustrated in Text-figs. 4 and 5, 10 weeks and 6 days after the extrusion of the planula (14.xii.28) from which it was derived. The corallites, in the centre have become well thickened; those at the periphery are still composed of relatively slight skeletal elements. $\times 9$.
- FIG. 2.—Skeleton of a colony formed from a wild planula which settled in a glass jar placed in about 5 fathoms of water near the mouth of the anchorage. The planula settled between 2.iv.29 and 28.vi.29, and the colony is therefore less than 12 weeks 3 days old, from the time of settlement. It illustrates the relatively stout form which wild colonies tend to assume, in contrast to the thinner disc-like condition more usually assumed by those reared on glass. $\times 27$.
- FIG. 3.—Two colonies, each consisting of a primary corallite surrounded by a circle of smaller corallites formed by buds (six in one case, five in the other). This represents the first stage in colony-formation, in its typical condition. The upper colony has a small worm-tube on it. Age of colonies, 7 weeks 4 days; extrusion of planulae, 13.ii.29. $\times 9$.
- FIG. 4.—A young wild colony derived from a planula which settled on a drain-pipe planted out in the Madreporite moat. The planula settled between 2.viii.28 and 28.v.29, and the colony is therefore less than 42 weeks 5 days old from date of settling. This figure illustrates the stage at which a sheet of corallites with well-thickened calices has been formed, but no upgrowth to form branches has yet taken place. The colony appears to have been formed by budding from a single primary polyp. The first bud of an incipient branch (S.E. of the primary polyp, and out of focus) has been formed. $\times 9$.
- FIG. 5.—A typical reared colony formed by one primary polyp and six primary buds. Note the slight ridge of irregular shape which surrounds the skeletons of the buds, a little way in from the margin of the basal plate (cf. fig. 6). Age of colony, 5 weeks 4 days; planula extruded 13.ii.29. $\times 12$.
- FIG. 6.—Skeleton of a reared colony with two primary polyps and 9 primary buds in two semicircles. Note the saucer-like ridge surrounding the white central part of the colony. The part outside the ridge had been killed by sediment and algae; the part inside the ridge was alive and healthy; and the ridge is interpreted as a reaction of the coral to sediment and algae (see p. 132). The ridge in fig. 5 is a slighter example of the same condition. Two worm-tubes have been formed on the dead part of the colony. Age of colony, 9 weeks 6 days; planulae extruded 13.ii.29. $\times 12$.
- FIG. 7.—Skeleton of a reared colony consisting of two primary polyps and 11 primary buds. In this case the whole outer parts of the colony had been killed by sediment and algae, and only two central areas (whiter than the rest and surrounded by delicate skeletal rings) were still alive. Three worm-tubes have been formed on the dead part, and attached to one end of the colony is the colony of a polyzoan, bearing another worm-tube. Age of colony 9 weeks 6 days; planulae extruded 13.ii.29. $\times 9$.

1

4

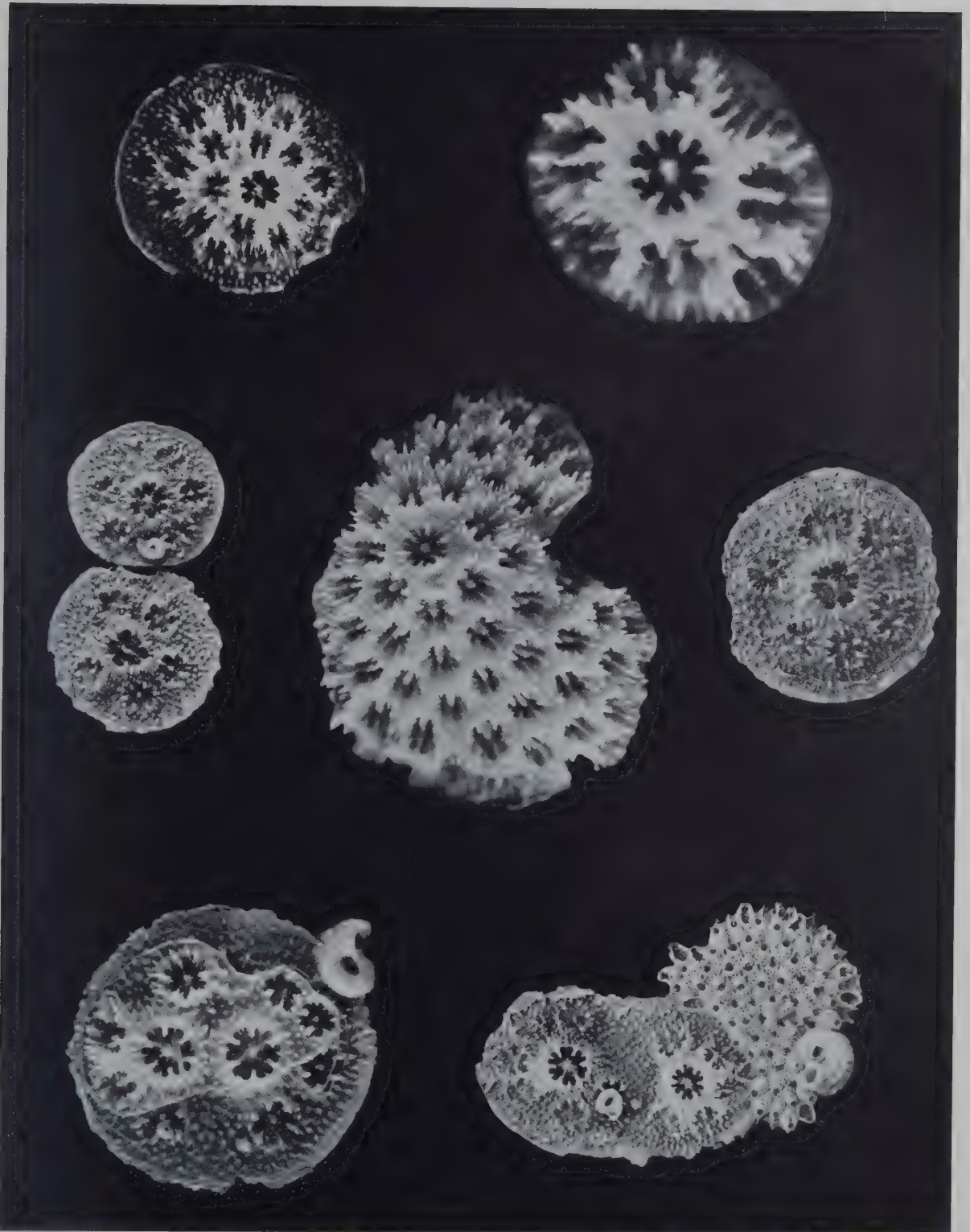
2

3

5

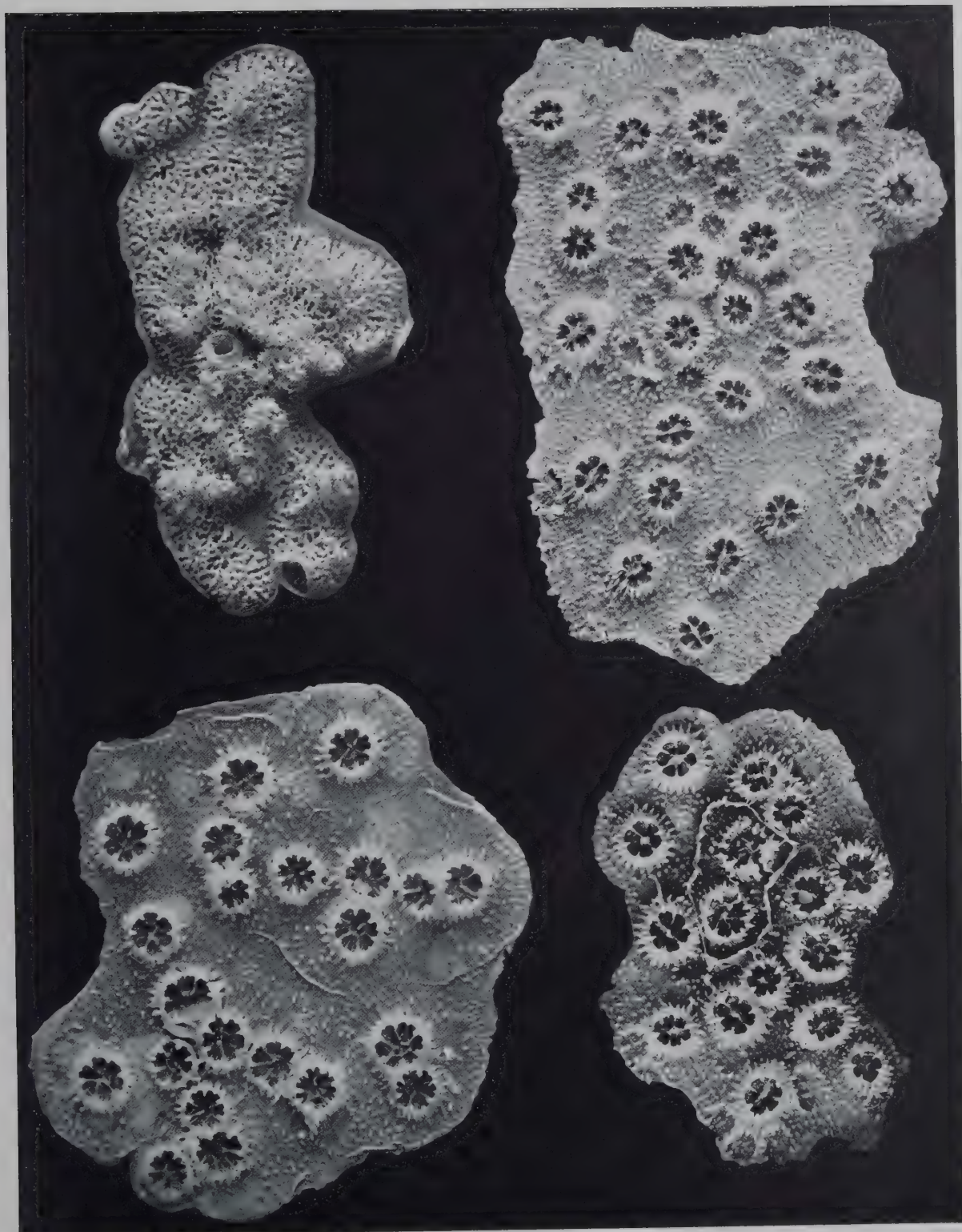
6

7



DESCRIPTION OF PLATE IV.

- FIG. 1.—Skeleton of a reared colony of *Porites haddoni*, formed by the fusion of a large number of primary polyps. In the upper left-hand corner two corallites have maintained their individuality; otherwise the corallites form an inextricable mass, among which individuals can be distinguished only approximately or not at all. Variation in the condition of the edge of the basal plate is well shown here—in some places it is flat, in others upturned, elsewhere masked by a strongly-developed inturned edge or parapet. Age of colony 3 weeks 3 days; planulae extruded 5.ii.29. $\times 9$.
- FIG. 2.—Portion of the skeleton of a large reared fusion-colony of *Pocillopora bulbosa*; it includes 25 primary corallites, and shows the relation to these of the skeletons of a number of buds. It shows also the thorny condition of the basal plate. Age of colony 5 weeks 4 days; planulae extruded 13.ii.29. $\times 9$.
- FIG. 3.—Skeleton of a reared fusion-colony of *Pocillopora bulbosa*, in a less advanced condition than that shown in fig. 2. The corallites of the primary polyps are less fully developed, and budding has only just started. The positions of some buds can be seen as clear places on the basal plate, free from spines. Age of colony about 5 weeks 5 days; planulae extruded on or about 15.xii.28. (Note that this colony is of the same age as that illustrated in fig. 2, but has developed less far in the time; probably because it was not put out in the sea at once after its formation.) $\times 10$.
- FIG. 4.—Another portion of the colony illustrated in fig. 2, showing a wall-like ring of coral surrounding two primary corallites, and probably induced by a local accumulation of algae and sediment. $\times 9$.



DESCRIPTION OF PLATE V.

- FIGS. 1-3 and 5-9.—Skeletons of young reared specimens of *Porites haddoni*. Those represented in figs. 1, 3, 7 and 9 were 4 weeks 5 days old when killed, and derived from planulae extruded 27.i.29; those in figs. 2, 5, 6 and 8 were 3 weeks 3 days old, from larvae extruded 5.ii.29. Fig. 1 shows a skeleton with only a slight development of marginal rim; fig. 2 a small one with a very strongly developed inturned rim; fig. 3 an intermediate. Fig. 5 shows a fusion between 2 primary corallites, with a strong marginal wall surrounding both; fig. 6 a similar case involving 3 corallites. Fig. 7 represents another 3-corallite colony, but here there are skeletal flanges between the corallites. Fig. 8 shows a fusion of 3 with very little marginal wall and no intrinsic flanges; fig. 9 a fusion of 4 corallites with well-developed flanges between them. Figs. 1, 2, and 5-9, $\times 9$. Fig. 3, $\times 12$.
- FIG. 4.—Skeleton of young *Pocillopora bulbosa* which had settled on materials planted out in the Madreporo moat. The materials were put out on 2.viii.28, the coral collected on 28.v.29; its age therefore cannot be more than 42 weeks 5 days, and is probably much less. $\times 9$.
- FIG. 10.—*Pocillopora bulbosa*. Drawing of the colony represented photographically in Plate III, fig. 2, showing further detail. Note the long columellae of the corallites formed by the 4 primary buds. $\times 51$.
- FIG. 11.—A group of young skeletons of *Porites haddoni*, in the natural positions taken up by the planulae in a finger-bowl. The largest colony was formed by fusion of a number of primary polyps, and has developed a system of twisted skeletal flanges. Skeletons 3 weeks 3 days old; planulae extruded 5.ii.29. $\times 6.5$.
- FIG. 12.—Colony of *Porites* from a larva (or larvae) which settled on clean materials fixed in a box in Porites pond. The box was put out 3.viii.28, and the coral collected 29.v.29; the age of the colony must therefore be less than 42 weeks 5 days. $\times 9$.
- FIG. 13.—Planulae of *Pocillopora bulbosa*, fixed in Bouin and preserved in alcohol. $\times 12$.

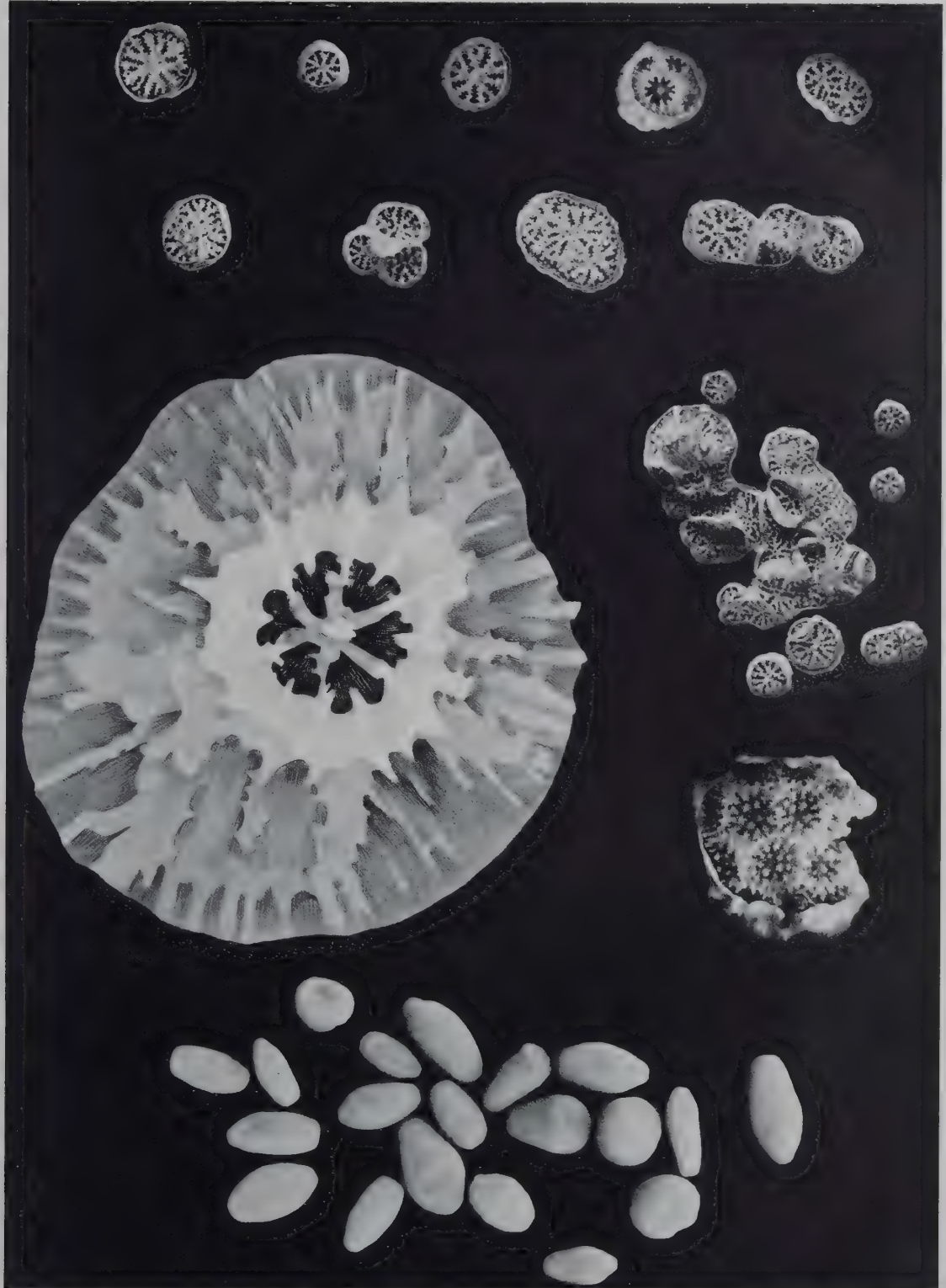
1 6 2 7 3 8 4 9 5

10

11

12

13



DESCRIPTION OF PLATE VI.

Pocillopora bulbosa.

The skeletons represented in figs. 1, 2 and 3 were laid down by colonies derived from planulae which settled on logs fixed in the Madrepore moat. These logs were placed in the sea 2 and 4.viii.28, and the colonies collected 28.v.29; their maximum age is therefore 42 weeks 5 days. The skeletons illustrated in the remaining figures are from a series of collected colonies to illustrate growth-stages; their age is not known. Fig. 9 shows a small adult colony; the remaining figures show stages of growth down to fig. 1, in which a mound has arisen on the sheet of young corallites, and is about to form the first branch. Figs. 1-3 show the development and subdivision of a single branch; figs. 4 and 5 the independent formation of more than one branch by the basal expansion; and figs. 6-8 stages between the initiation of branching and the adult condition. Figs. 1-5 illustrate to some extent the difference in form between the calices on the basal expansion and those (*a*) on the stalk and (*b*) towards the apex of branches.

Scale of figures.

Figs. 1 and 2, $\times 5$ diams.; figs. 3-5, $\times 4$ diams.; figs. 6-8, $\times 2$ diams.; fig. 9 is reduced, the actual coral measuring 17.5 cm. in diameter.

1

4
6
7

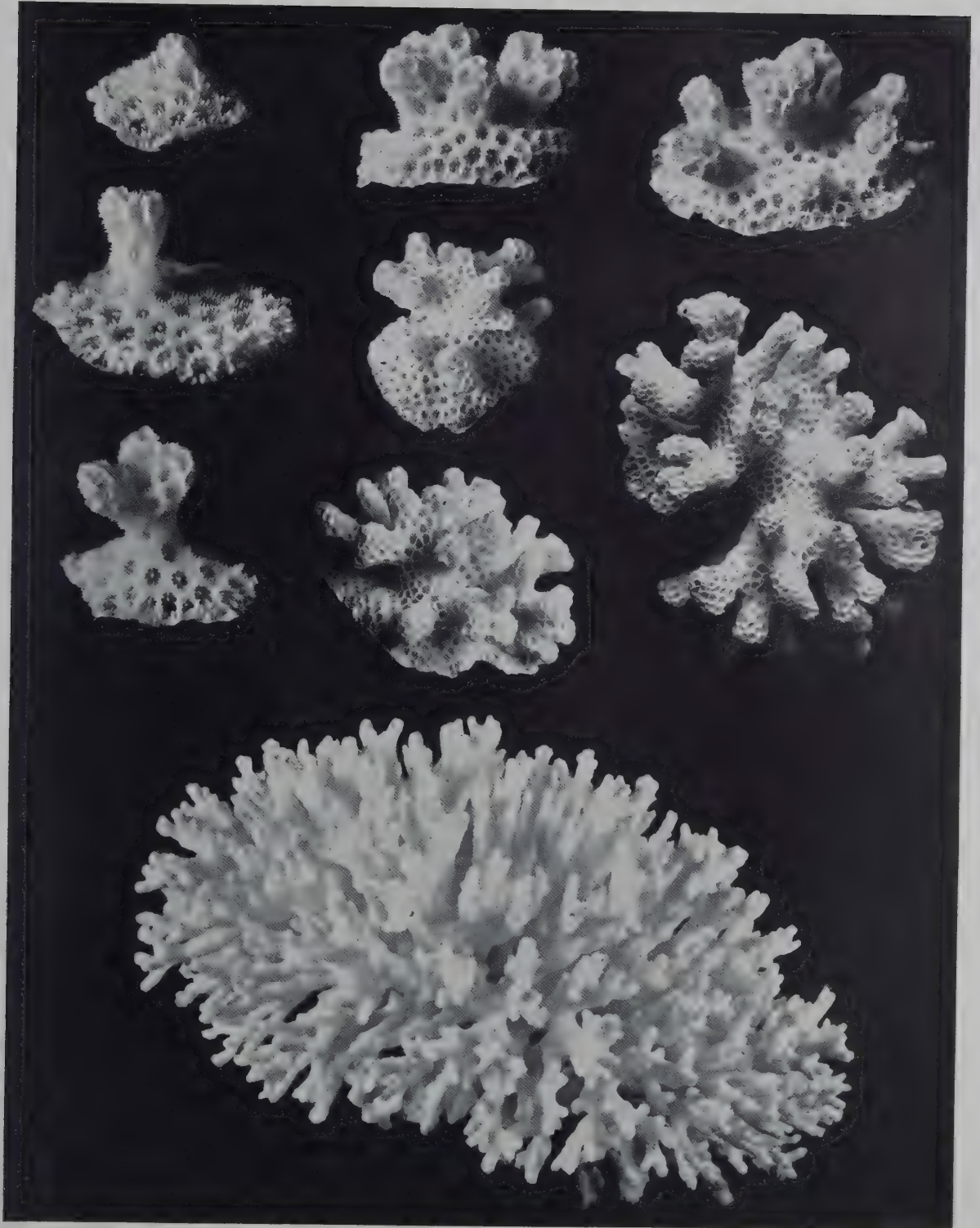
5

2

3

8

9



OBSERVATIONS ON THE LIFE-HISTORY AND DEVELOPMENT OF THE HYDROID, MYRIONEMA AMBOINENSE

BY

ELIZABETH A. FRASER, D.Sc.,

Senior Lecturer, Department of Zoology, University College, London

WITH SIX TEXT-FIGURES AND THREE PLATES

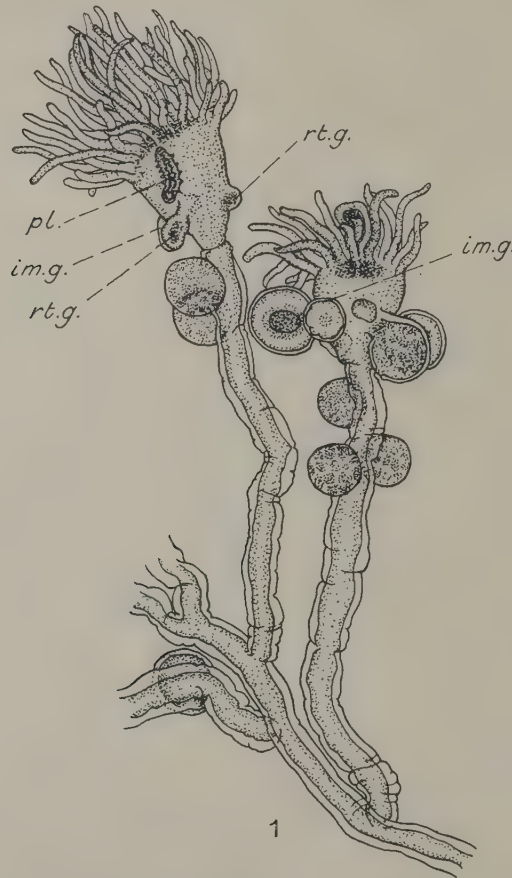
Myrionema amboinense (Pictet,* 1893) is found abundantly on Low Island, Queensland, in the shallow water along the margin of the mangrove swamp, especially the north-west corner (Key Chart of Low Isles, P. 1). The green plants *Thalassia hemprichii* and *Halimeda opuntia* are plentiful over the same area, and the hydroid grows in tufts on these plants and on the submerged roots of the mangrove trees, as well as on small sponges or on empty shells. The tufts average 1.5 cm. in height, but may be considerably taller (up to 4 cm. or more). Apart from the larger animals, such as the long snake-like holothurian, *Synapta maculata*, numbers of which creep continually along the ground, there is a smaller fauna living among the stems of *Myrionema* itself. Most characteristic is a small Tanaid crustacean *Leptochelia savignyi* (Krøyer), which is invariably present, inhabiting a gelatinous tube fixed to a part of the stalk, or sometimes crawling freely over the branches. Many small foraminifera are quite common, as well as the large conspicuous *Orbitolites complanata*, which sticks to the fronds of the two plants.

In 1913, Light* described this same hydroid under the name of *Eudendrium griffini* as occurring in shallow tide channels on the coral reef of Bantayan Island, Philippine Islands. All his descriptions and figures are based on preserved material, consisting of one female and one male colony bearing gonophores and four immature colonies.

Myrionema was one of a number of common forms found on Low Island which were selected by Dr. T. A. Stephenson for the determination of their breeding periods. For this purpose I undertook the weekly examination of this species during four months from March to June, and had therefore an opportunity of observing the animal closely. Some interesting details in the life-history, as seen in the living hydroid, are here recorded, as well as observations on the development as investigated by sections of specimens preserved in Bouin's fluid. Fresh material was collected every few days, and in this way most of the developmental stages were secured; colonies did not flourish when kept under artificial conditions. Recently-hatched planulae were placed in finger-bowls in which the sea-water was changed twice a day; it was then possible to watch their transformation into the polyp.

* I am indebted to Dr. E. A. Briggs, of Sydney University, for the correct name of the hydroid and for referring me to the paper by Light. Dr. Briggs's report on the Hydroids will be published in Vol. IV of this series.

According to Light, a characteristic feature of the male is that two gonophores are commonly borne on each hydranth. Although two is certainly the most prevalent number, very many hydranths, in a colony that is obviously flourishing, bear only one; three is also quite usual (Plate I, figs. 1 and 2), whilst rarely even four are present. The gonophore consists of two, three or four chambers (Plate I, figs. 1 and 2), sometimes only one, and, as



TEXT-FIG. 1.—Drawing of a cleared preparation from part of a female colony showing two hydranths. One bears a very immature gonophore (*im.g.*) and two embryos fixed to its stalk; the remains of two depleted gonophores (*rt.g.*) project from the body, and within the coelenteron is a small polychaete (*pl.*). The second hydranth has three embryos fixed alternately down the stalk and a fourth is just ready to be attached; two well-developed gonophores and one immature one (*im.g.*) are borne on its body. $\times 25$.

recorded by Light, it may be bifurcated at the tip. Active spermatozoa were observed in gonophores of all sizes.

In the female, four to six gonophores to a hydranth is the typical condition, but in some colonies a much greater number may be seen crowded round the lower portion of the polyp. In the specimen figured (Plate I, fig. 3) ten well-developed gonophores were

counted; seven were very commonly present, and these may be at different stages of development, as for example in one case where five occurred round the hydranth, of which two were not fully formed, whilst an additional three were in the act of being placed upon the stalk immediately below. Variable numbers of gonophores are shown in Text-figs. 1 to 4.

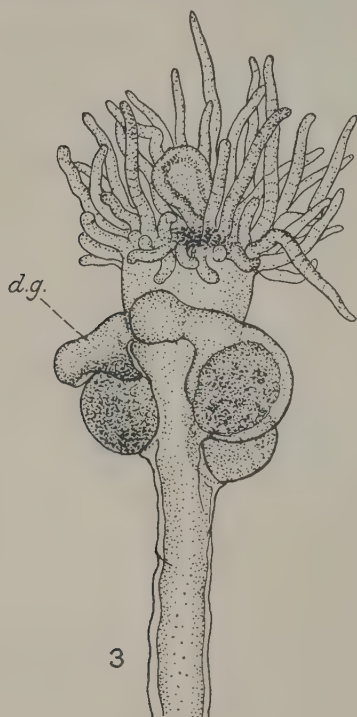
The process by which the ovum reaches the stalk is an interesting one. The gonophore, when fully developed, consists of a hollow outgrowth of the hydranth containing



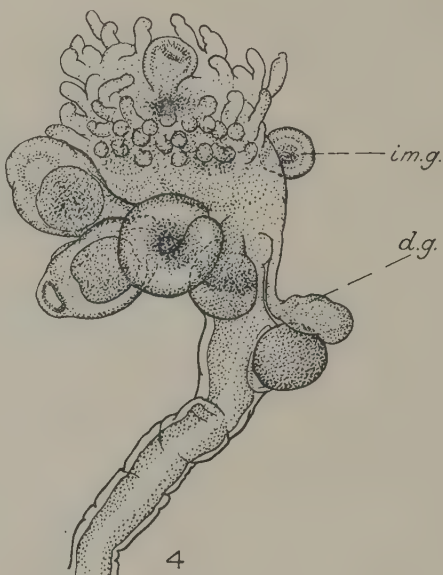
TEXT-FIG. 2.—Drawing of part of a preserved colony showing three stalks carrying a variable number of embryos; their gonophores are reduced to mere stumps (*rt.g.*), which project from the body of the two hydranths. Each hydranth bears a well-developed gonophore. The hydranth has disappeared from the third stalk. $\times 25$.

both ectoderm and entoderm, between which is an extremely thin layer of mesogloea. The entodermal spadix encircles the ovum in the shape of a horseshoe, at the open end of which the ovum is only separated from the exterior by a thin layer of ectoderm, very much as figured by Allman (1871) (Plate XIII, fig. 6) for *Eudendrium ramosum*. On reaching a certain stage, the pedicel of the gonophore bends downwards so as to press the open side of the spadix against the hydrocaulus, the thin layer of ectoderm in this

region simultaneously disappearing, apparently by actual rupture, and possibly also by partial disintegration. The ovum thus exposed adheres immediately to the perisarc of the stem by the tough capsule it has by this time secreted around itself. The spadix simultaneously contracts so that its two layers come into contact and its cavity is obliterated (Plate II, fig. 7, *sp.*); the empty gonophore now springs back to its former position as a transparent cap (Text-figs. 3 and 4), which shrinks rapidly, and all that remains is a short stump which projects from the body of the hydranth for some time afterwards (Text-figs. 1 and 2, *rt.g.*). I have never seen any part of the depleted gonophore drop off;



TEXT-FIG. 3.



TEXT-FIG. 4.

TEXT-FIG. 3.—Drawing of a cleared preparation of a female hydranth, showing an ovum which has just become fixed to the stalk. The empty gonophore (*d.g.*) is springing back as a transparent cap. A second ovum is about to be placed on the stalk (the pedicel has been displaced to one side by the coverslip), and a third embryo is already attached to it. $\times 40$.

TEXT-FIG. 4.—Drawing of a cleared preparation of a female hydranth, showing a relaxed gonophore with a lengthened pedicel (*d.g.*). Seven other gonophores are present, two of which are only indicated behind the hydranth; all are well developed except one (*im.g.*), which is quite small. $\times 40$.

the cord-like spadix becomes withdrawn into the hydranth and the ectoderm shrivels markedly, whilst both layers appear to undergo a considerable amount of degeneration. The ova may be affixed to the stalk in an irregular ring just below the hydranth (Text-fig. 2) or alternately down the stem (Text-figs. 1 and 2), the latter being the more usual method. In order to attach the ovum at lower levels the pedicel of the gonophore lengthens so that the requisite position may be reached (Text-fig. 4), the hydranth itself often

bending over at the same time, thus aiding in the operation. This process is certainly not due to early atrophy of the polyp as suggested by Light, for gonophores at varying stages of development frequently occur around the same hydranths (Text-figs. 1 and 4). Some may be quite small, others large, and yet others may have already deposited their ova down the stem. When all these have been placed on the stalk the hydranth frequently dies off, but by no means always. In one interesting example, where two embryos were developing on the stalk, the hydranth was not only flourishing, but young ova were observed in the ectoderm, a short distance below these embryos. It may be noted also that the polyp shown in Text-fig. 1 was actively feeding, as shown by the polychaete in its coelenteron.

I have not attempted in this paper to go into the question of the origin of the germ-cells, whether they arise from the ectoderm or the entoderm—a point about which in hydroid there is still much difference of opinion. The question is not of much importance, however, as Goette (1907) has shown that the place of origin differs according to the genus or even according to the species, and that in *Eudendrium* it may perhaps vary in one and the same species. In *Myrionema* both large and smaller ova each containing a reticular nucleus and a conspicuous nucleolus are to be seen along the stalks of the hydranths; everyone of these lies in the ectoderm close against the mesogloea (Plate I, fig. 4a, ov.). In a developing bud (Plate I, fig. 4, ov.) or in the fully formed polyp (Plate I, fig. 5, ov.), on the other hand, ova are invariably found within the entoderm. Similar observations have been made by Congdon (1906) in *Eudendrium hargitti*, and therefore this author concludes that the egg must pass through the mesogloea at the neck of the hydranth. There is no doubt that the ova do penetrate through the mesogloea in this region, for I have actually seen the migration taking place. Plate I, fig. 5, shows a transverse section through the stalk just below the hydranth; lying in the ectoderm is an ovum from which pseudopodial processes extend out into the entoderm, the mesogloea having disappeared along this area. Migration from the ectoderm into the entoderm has been described in several hydroids, but the actual penetration through the mesogloea has not always been observed, and it usually occurs when the egg is at an earlier stage, and therefore much smaller in size than in *Myrionema*.

Great difficulty was experienced in trying to follow the development of the egg into the planula. C. W. Hargitt (1904) found it impossible to make out the early cleavage stages in *Eudendrium ramosum* owing to the apparently complete disappearance of the nucleus. The same phenomenon occurs in *Myrionema*, and here observations are rendered much more difficult by the presence of algal cells. These zooxanthellae have already been described by Light (1913). They are present in large numbers at the base of the entoderm cells and are crowded together in the tentacles. Ova lying in the ectoderm of the stalk very rarely contain zooxanthellae—actually in one case only were such cells seen within the ovum at this stage, and the infection was already well established, for no less than 23 to 24 algae were counted—but as soon as the ovum passes into the entoderm of the hydranth numerous algal cells come to lie within the cytoplasm. Once within the gonophore they undergo multiplication, obscuring still further the inconspicuous nuclear divisions.

Many staining methods were tried, the zooxanthellae standing out well after safranin counterstained with gentian violet and iodine (Gram's method), and still better after Volkonsky's stain; safranin with Wasserblau, and also iron brazelin were found useful;

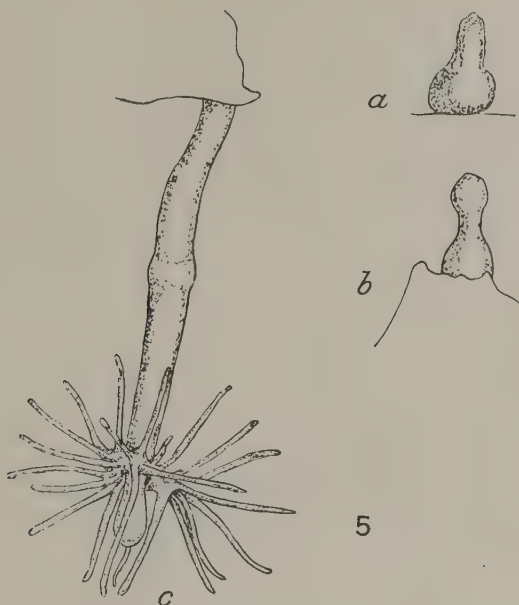
but on the whole iron haematoxylin gave the best results, preferably the quick method, care being taken that the yolk was left quite pale in colour.

On reaching the entoderm of the hydranth the outline of the egg becomes indistinct and tends to merge into the surrounding entoderm cells. Not only zooxanthellae, but entoderm cells also appear to become incorporated into the cytoplasm of the ovum. These entoderm cells are exceedingly small and it was impossible to follow their subsequent fate, but very probably they contribute towards the formation of yolk, as they are known to do in some other hydroids. It may be noted here that occasionally a few ectoderm cells appear to be present in the cytoplasm of young ova which are migrating along the stalk, but the part, if any, these play in later development it is impossible to say. As soon as the ovum becomes enclosed within the gonophore, yolk increases very rapidly in amount, but I have no definite evidence that the entoderm cells of the spadix participate in this increase, as inferred by C. W. Hargitt (1904). Entoderm cells can be distinguished round the periphery of the egg during accumulation of yolk, but soon their identification is no longer possible. The zooxanthellae are at first also scattered near the margin (Plate II, fig. 6, z.), and may be rather more numerous about the nucleus of the ovum.

The yolk soon divides up into small spheres, a mass of compact yolk forming in the centre (Plate II, fig. 6), but by the time the egg is ready to leave the gonophore this central portion has also split into spheres. The nucleus, which has a conspicuous nucleolus and a fine chromatin network, originally lies near the centre, but when a large quantity of yolk has been produced, it passes to the margin of the ovum (Plate II, fig. 6, n.). The nuclear membrane very soon breaks down, the nucleolus disappears and the nuclear contents disperse as fragments, and all traces of these are lost. This condition, however, only lasts for a very brief period; almost as soon as, or even before, the partition of yolk into spheres is complete and the ovum has become attached to the stalk, irregular patches of protoplasm of comparatively large size are visible between the spheres (Plate II, fig. 7). In many of these definite chromosomes are discernible, whilst stages of mitosis can be recognized (Plate II, fig. 8). From the protoplasmic masses amoeboid processes extend out, and these continue into delicate prolongations which penetrate between the spheres, constituting a slender reticulum. This network is not easy to follow, but most probably it is present throughout the egg, uniting the protoplasmic masses. The yolk spheres gradually collect together into a number of circular clumps, in each of which are included a few algal cells, and within each also one of the protoplasmic masses is usually to be seen (Plate II, fig. 9). In all likelihood every ball of yolk spheres contains such a mass, although I was unable to demonstrate its presence in every case. On bursting the capsule in living material these balls were mistaken for early blastulae, each composed of a number of cells, but sections subsequently showed that apart from zooxanthellae the supposed cells were simply spheres of yolk, the protoplasmic masses and strands not being easily perceptible, and, moreover, were not suspected at the time.

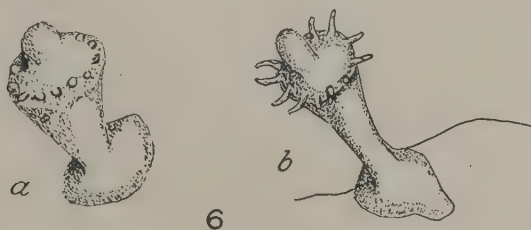
As development proceeds within the capsule the embryo becomes more solid, the yolk-balls unit together, and the protoplasm spreads out more evenly throughout the egg. Eventually it tends to accumulate round the margin, at first in an ill-defined manner (Plate III, fig. 11), but gradually becoming transformed into a distinct ectodermal layer (Plate III, fig. 12), which originates at one side or another, and by degrees develops round the entire surface. During the formation of the ectoderm an irregular cavity appears in the centre of the embryo. The capsule now very soon ruptures (Plate III, fig. 13), and the

larva creeps out as a planula (Plate III, fig. 14), the central cavity rapidly enlarging. This takes place only a few days—the exact number was not definitely determined—after the capsule is fixed to the stalk of the hydranth. The planula never swims freely in the



TEXT-FIG. 5.—Drawing of a living young hydroid, specimen B. *a*, The pear-shaped planula immediately after fixation, 24 hours after hatching; *b*, the same, 30½ hours after hatching; *c*, the same, 5 days after hatching, when it measured about 2 mm. from the base to the tip of the hypostome.

water, but slowly creeps by means of mucus secreted by cells of the ectoderm, and drops on to neighbouring plants or on to other *Myrionema*, or apparently may crawl along the stalk of the parent colony. It is difficult to be quite sure that cilia are absent, but certainly after careful observations none were detected. Movement is at all events very



TEXT-FIG. 6.—Drawing of a living young hydroid, specimen A. *a*, 24 hours after hatching; *b*, 30½ hours after hatching.

restricted, and if a suitable surface on which a planula can attach itself is not almost directly reached, it soon perishes. Favoured by a convenient substratum it becomes pear-shaped and then fixes itself by the broad end (Text-fig. 5, *a*). At this end a cone-shaped plug of entoderm (Plate III, fig. 14) can be seen for some time projecting into the

central cavity. The time taken for further growth varies slightly, at least when confined within a finger-bowl. The fixed end spreads out, and at about 24 hours after hatching the young hydroid assumes the shape seen in Text-fig. 5, *a*, and may even have developed tentacular buds (Text-fig. 6, *a*). Text-figs. 5 and 6 show two specimens which fastened themselves to a small piece of *Halimeda* weed, specimen A having developed rather more quickly than specimen B. The latter is depicted in Text-fig. 5, *c*, five days after hatching, when it measured about 2 mm. from the tip of the hypostome to the base of the animal. Owing probably to unfavourable conditions the head of A died off between three and four days after hatching, but nine or ten days later a new head was found to be developing, which in 24 hours showed a distinct hypostome and a circle of small tentacular knobs; two days afterwards, however, degeneration again set in and no further regeneration occurred.

DISCUSSION.

The development of *Myrionema* shows a striking resemblance to that described in *Distichopora* by Hickson (1893). There the nucleus migrates to the edge of the gonophore, the nuclear membrane disappears and the nuclear contents are scattered throughout the ovum. Islands of protoplasm next appear in the yolk, and these are connected by a very coarse network of fine protoplasmic strands; later these islands become more numerous and the network finer. A syncytium is eventually formed round the periphery from which the ectoderm is differentiated. Nests of yolk similar to those seen in *Myrionema* are described and figured, but in *Distichopora* this segmentation is believed to affect the yolk only, for the nuclei are always distributed between the aggregations of yolk.

C. W. Hargitt (1904) has given an account of the development of *Eudendrium ramosum*, and in many details it corresponds to that of *Myrionema*. Hargitt describes the massing of the yolk towards the centre of the gonophore, due as he thinks to formation of yolk round the periphery by the metabolism of the entodermal cells of the gonophore. In *Myrionema* also entoderm cells seemingly become enclosed within the egg and presumably participate in the genesis of yolk, but as already mentioned, it is uncertain if the actual spadix takes part in this process. A similar migration of the nucleus to the margin and subsequent fragmentation occurs in *Eudendrium ramosum*, but there a cytoplasmic reticulum still remains throughout the egg, no such reticulum being observed in *Myrionema* at this stage. The accumulation of yolk into balls also takes place, and only in some of them were nuclear centres discernible, so that division of the yolk here likewise appears to have some relation to the protoplasm. The large masses of protoplasm often containing nuclear divisions, so conspicuous in *Myrionema* and corresponding so closely to those figured for *Distichopora* by Hickson, are not definitely described for *Eudendrium ramosum*. The ectoderm is formed as in *Myrionema*, but the larva is ciliated and has a longer free-swimming life, up to three days, and probably owing to this fact the entoderm is not differentiated so early—not until near the time of fixation.

The shifting of the nucleus to the periphery of the egg and the subsequent discharge of the nuclear constituents is a common phenomenon in hydroids, and is closely related to the process of maturation and of fertilization. Neither maturation nor fertilization were observed in *Myrionema*; quite possibly fertilization takes place at night, as discovered by Benoit (1925) in *Myriothele*.

The zooxanthellae (Plate II, fig. 10) in *Myrionema* are most numerous in the tentacles,

but are present in large numbers in the entoderm of the polyp and along the stem; they occur more sparingly in the hypostome and in the entodermal lobes round the base of the hypostome. In all these situations they can be seen undergoing division into two, the pyrenoid first and then the nucleus. In some specimens division into three also takes place, especially in the tentacles where multiplication is most active, the nucleus of one of the daughter cells undergoing a second division. In this connection it is noteworthy that the zooxanthellae present among the yolk spheres of the developing embryo often lie in groups of three cells. Division into four was never observed anywhere.

Zooxanthellae very similar to those found in *Myrionema* have been described and figured in *Millepora* by Mangan (1909). A pyrenoid can always be seen surrounded by a clear space, and the nucleus is spherical with closely packed chromatin granules. The cell membrane did not respond to cellulose tests, and it may be noted that in *Myrionema* it was found impossible to get the wall to take on the usual cellulose stains. In *Myrionema* the algal cells pass into the ovum as soon as the latter begins to migrate into the entoderm, and there soon multiply rapidly; in *Millepora* they lie in the vacuolated substance of the manubrium, and from thence pass directly into the ovum, here undergoing division into two, and occasionally four cells. As already stated, division into four was never seen in *Myrionema*.

As early as 1882 Hamann figured the green cells moving from the entoderm through the mesogloea into the egg of *Hydra viridis*, and later workers (Hadzi, 1906; Goetsch, 1919) have confirmed these observations. In 1911, Hadzi showed that the xanthellae in *Halecium ophiodes*, penetrating the mesogloea, make their way from the entoderm of the gonophore into the egg. The most recent investigator (Haffner, 1925) of *Chlorohydra viridissima* (formerly *H. viridis*) has demonstrated very clearly (Text-fig. 16, p. 43) the manner in which large numbers of chlorellae migrate from the entoderm through the mesogloea to the ovum. It has been mentioned that in an isolated case in *Myrionema* zooxanthellae were present within an ovum which lay in the ectoderm of the stalk; these must have travelled through the mesogloea, so that a method of infection similar to that in *Hydra* may occur very exceptionally in *Myrionema* also.*

In his original description of *Myrionema* Pictet (1893) gives the colour as yellow-green. In the same species from Ceylon green cells comparable with *Chlorella vulgaris* have been described by Svedelius (from Oltmann, 1923). It is thus evident that *Myrionema amboinense* may contain either zoochlorellae or zooxanthellae according to the locality in which it is found.

I am much indebted to Miss Joyce Townend for the drawings of Text-figs. 1 to 4 and of Plate I, fig. 3. I have also to thank Mr. F. J. Pittock, of University College, for the microphotographs, Plate I, figs. 1 and 2.

REFERENCES.

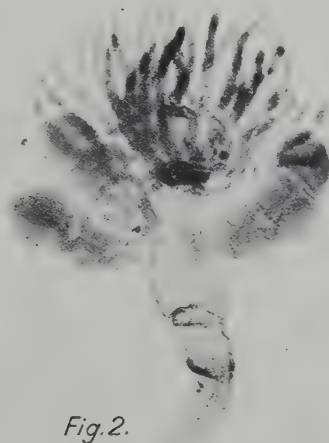
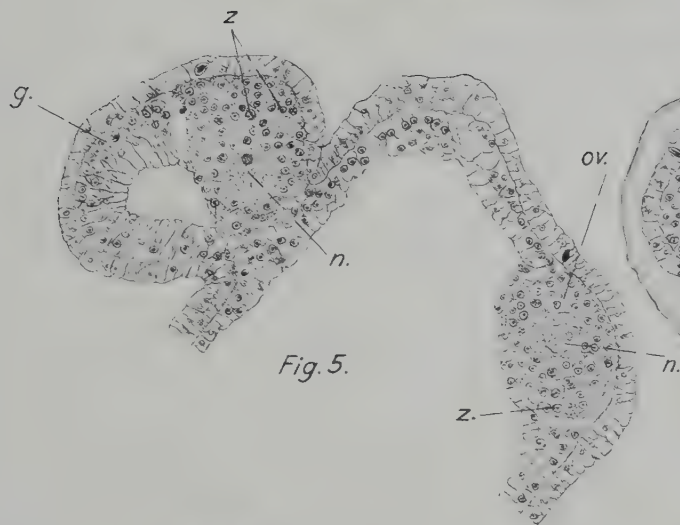
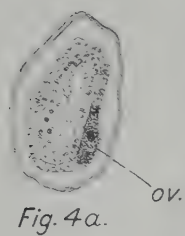
- ALLMAN, G. J. 1871-1872. A Monograph of the Gymnoblasic or Tubularian Hydroids. Ray Society, 2 pt. illustrations.
 BENOIT, P. 1925. L'Ovogenèse et les premiers stades du Développement chez la Myriothele et chez la Tubulaire. Arch. Zool. exp. gén. LXIV, pp. 85-326, pls. iii-xii, text-figs. 1-65.
 CONGDON, E. D. 1906. Notes on the Morphology and Development of Two Species of *Eudendrium*. Biol. Bull. Wood's Hole, XI, pp. 27-46, text-figs. 1-11.

* I understand that Dr. Briggs has occasionally observed algae in the ectoderm.

- GOETSCH, W. 1919. Neue Beobachtungen und Versuche an Hydra: II Teil. Biol. Zbl. XXXIX, pp. 544-557, text-figs. 1-7.
- GOETTE, A. 1907. Vergleichende Entwicklungsgeschichte der Geschlechtsindividuen der Hydropolypen. Z. wiss. Zool. LXXXVII, pp. 1-335, pls. i-xviii.
- HADZI, J. 1911. Über die Symbiose von Xanthellen und *Halecium ophiodes*. Biol. Zbl. XXXI, pp. 85-96.
- HAFNER, K. v. 1925. Untersuchungen über die Symbiose von *Dalyellia viridis* und *Chlorohydra viridissima* mit Chlorellen. Z. wiss. Zool. CXXXVI, pp. 1-69, pl. i, text-figs. 1-27.
- HAMANN, O. 1882. Zur Entstehung und Entwicklung der grünen Zellen bei Hydra. Z. wiss. Zool. XXXVII, pp. 457-464, pl. xxv, i.
- HARGITT, C. W. 1904. The Early Development of *Eudendrium*. Zool. Jahrb. Anat. XX, pp. 257-276, pls. xiv-xvi.
- HARGITT, G. T. 1913. Germ-Cells of Coelenterates. J. Morph. XXIV, pp. 383-414, pls. i-iii.
- HICKSON, S. J. 1893. The Early Stages in the Development of *Distichopora violacea*. Quart. J. Micr. Sci. XXXV, pp. 129-158, pl. ix.
- LIGHT, S. F. 1913. The Morphology of *Eudendrium griffini* sp. nov. Philipp. J. Sci. D. VIII, pp. 333-356, pls. i, ii, text-figs. 1-5.
- MANGAN, J. 1909. The Entry of Zooxanthellae into the Ovum of Millepora, and Some Particulars Concerning the Medusa. Quart. J. Micr. Sci. LIII, pp. 697-709, pl. xviii.
- OLTMANN, FR. 1923. Morphologie und Biologie der Algen. III, p. 508, Jena.
- PICOT, C. 1893. Étude sur les Hydres de la Baie d'Amboine. Rev. Suisse Zool. Genève I, pp. 1-64, pls. i-iii.

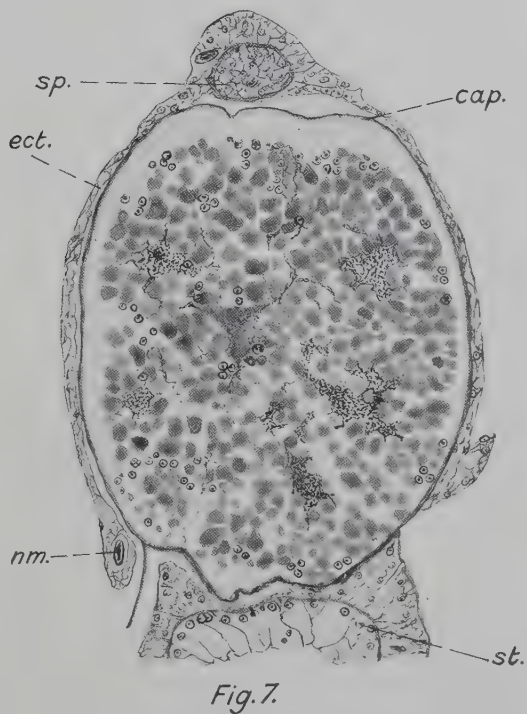
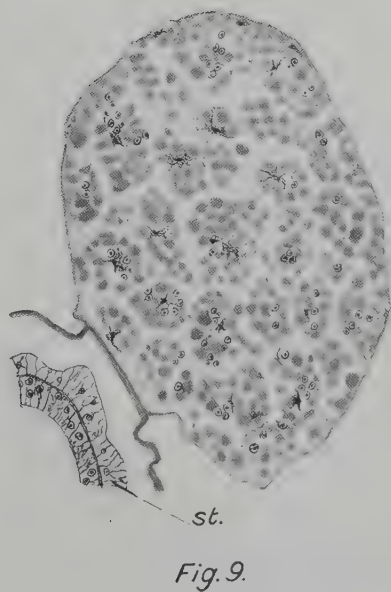
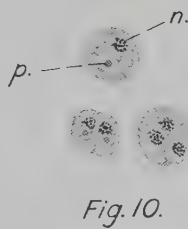
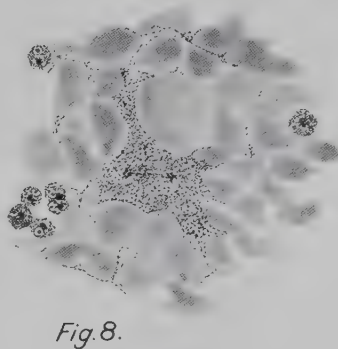
DESCRIPTION OF PLATE I.

- FIG. 1.—Photograph of a male hydranth bearing three ripe gonophores, one composed of 3, the other two of 4 chambers. $\times 20$.
- FIG. 2.—Microphotograph of a cleared specimen of a male hydranth bearing three gonophores, one composed of 4, and two of 3 chambers. $\times 30$.
- FIG. 3.—Drawing of a female hydranth bearing ten fully developed gonophores, of which eight are visible, in whole or part. $\times 25$.
- FIG. 4.—Longitudinal section through a bud showing three ova (*ov.*) lying within the entoderm. A few zooxanthellae (*z.*) are seen in the cytoplasm of the ova. $\times 110$.
- FIG. 4a. Transverse section through the stalk a short distance below fig. 4, showing an ovum (*ov.*) lying in the ectoderm. $\times 110$.
- FIG. 5.—Section passing obliquely through a hydranth and transversely through the stalk immediately below it. One ovum (*ov.*) is seen lying in the entoderm, and another has just passed into a developing gonophore (*g.*). In both the nucleus is shown, and numerous zooxanthellae (*z.*) lie in the cytoplasm. An ovum (*ov.*) lies in the ectoderm of the stalk and from it pseudopodial processes are penetrating into the entoderm, the mesogloea having disappeared in this region. One zooxanthella (*z.*) has already passed into the cytoplasm. $\times 110$.



DESCRIPTION OF PLATE II.

- FIG. 6.—Section through a fully developed gonophore, showing the hollow thick-walled spadix (*sp.*) surrounded by the ectoderm. Within lies the ovum. The nucleus (*n.*), showing a well-marked nucleolus, has migrated to the margin, and the yolk consists of a central mass surrounded by yolk-spheres. The zooxanthellae (*z.*) are seen round the circumference. $\times 200$.
- FIG. 7.—Section through a developing embryo immediately after its attachment to the stalk. Large protoplasmic masses can be seen among the yolk spheres, and in some of these chromosomes or masses of chromatin are present. Zooxanthellae (*z.*) are scattered among the yolk. The ectoderm (*ect.*) of the gonophore is retracting and the spadix (*sp.*) is reduced to a solid cord of cells. *cap.* = capsule. *nem.* = nematocyst. *st.* = stalk. $\times 200$.
- FIG. 8.—Section through a protoplasmic mass a few sections behind fig. 7, showing a telophase of mitosis. Several zooxanthellae (*z.*) are drawn, containing a darkly staining nucleus and a well-marked pyrenoid. Some are undergoing division. $\times 600$.
- FIG. 9.—Section through an embryo at a later stage than Fig. 7. The yolk-spheres have collected into a number of balls, within some of which protoplasm containing chromatin is visible. *st.* = stalk. $\times 200$.
- FIG. 10.—Three zooxanthellae. One is undergoing division into two, and in another there are three nuclei. *n.* = nucleus. *p.* = pyrenoid. $\times$ about 1200.



DESCRIPTION OF PLATE III.

- FIG. 11.—Section through a later stage than fig. 9. The protoplasm is now beginning to accumulate round the periphery of the embryo, especially at one side. $\times 200$.
- FIG. 12.—Section through an embryo in which a definite layer of ectoderm has formed round the side adjacent to the stalk. A central cavity has made its appearance. $\times 200$.
- FIG. 13.—Section through a planula about to hatch. The ectoderm is well developed and laden with mucus-cells, and there is a well-marked central cavity. The capsule is ruptured at one side, and opposite this area mucus is being actively secreted; this strongly suggests that mucus plays a part in the dissolution of the capsule. $\times 200$.
- FIG. 14.—Longitudinal section of a planula immediately after hatching. A plug of entoderm is seen projecting into the cavity at one end. $\times 110$.

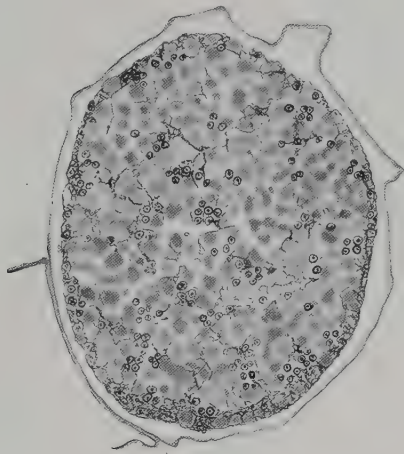


Fig. 11.



Fig. 12.

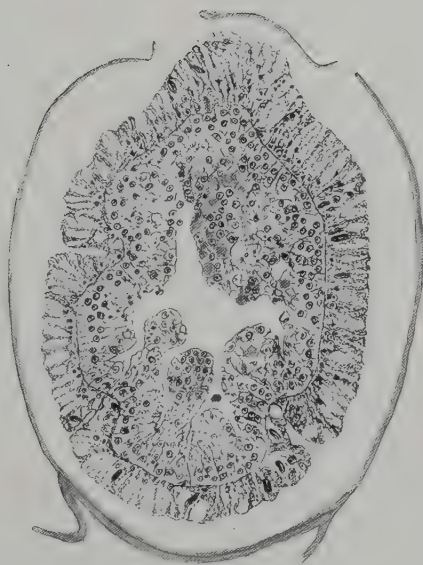


Fig. 13.

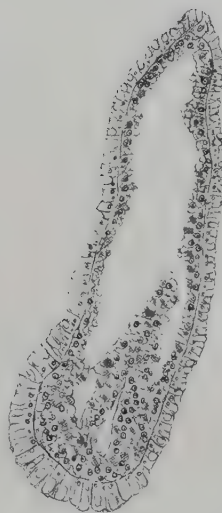


Fig. 14.

NOTES ON TROCHUS NILOTICUS

BY

F. W. MOORHOUSE, B.Sc.

Marine Biologist to the Government of Queensland

CONTENTS

	PAGE
1. INTRODUCTION	145
2. DESCRIPTION	145
3. HABITAT	146
4. GROWTH RATE AND AGE	148
5. REPRODUCTION	153
6. SUMMARY	155
7. REFERENCES	155

1. INTRODUCTION.

Trochus niloticus is a primitive gastropod belonging to the Rhipidoglossa. In Queensland it is found on all the reefs and cays of the Great Barrier Reef, and its attendant lagoon channel, from Mackay to the New Guinea coast, as well as on many of the continental islands in this area and in the Torres Straits. The islands of the East Indies, the Coral Sea, New Guinea, Fiji and New Caledonia also produce it in large numbers. On the northern shores of West Australia it is found in much smaller numbers. It appears to be confined to the Tropical West Pacific and the Indo-Pacific regions.

Throughout this paper wherever *Trochus* is mentioned it is intended to refer solely to the species *T. niloticus*.

I desire here to record my thanks to the late Premier of Queensland, the Hon. W. McCormack, for giving me the opportunity to leave Brisbane with the Expedition, to Prof. E. J. Goddard for advice and the loan of apparatus, and to various fellow-members of the Expedition for advice and assistance.

2. DESCRIPTION.

The anatomy of the European species of *Trochus* has been studied by Robert (1900) and Randles (1904). A description of the shell of *Trochus niloticus* together with some excellent photographs was published by Hedley (1917), so that it need not be given here. His statement that there is a grotesque expansion of the last whorl of a *Trochus* shell,

however, applies only to those shells which are over 8 cm. in diameter. Up to that size the shell is straight-sided.

When the animal is examined in its shell, but with the foot and body protruded as in walking, there is seen a very large foot, which bears sensitive papillae over the greater part of its upper surface. The epipodium bears fine retractile cylindrical tentacles, six on each side, each arising from a small notch or indentation. The foot can be grooved from front to rear, so that the two sides become apposed when the animal retracts within its shell. On the posterior part of the foot is a brown, horny operculum.

The head bears a pair of tentacles, a pair of ocular peduncles, a pair of cephalic lobes and a small muzzle, very short and non-retractile. The mouth is terminal and the lower part is cleft, giving the appearance of two lateral lips. Within the buccal cavity is a many-toothed radula, typical of all "scraping" gastropods (Yonge, 1928). This works over two cartilaginous plates situated on the floor of the buccal cavity. In action the radula is forced through the mouth, which loses its slit-like form and becomes rounded. The radula is drawn from top to bottom of the mouth, giving a final upward lick just as the lips close.

On the outer side of the shell-mouth—that is, on the left side of the animal—there can be extruded a portion of the mantle, which, folding slightly, forms temporarily a short exhalent siphon, while on the inner side of the body near the columella there is a similarly formed inhalent siphon.

When the animal is taken from its shell most of the principal organs can be seen through the thin mantle. The most noticeable feature is the coiled stomachal caecum, which, being brown and approximately the size of a threepenny-piece, stands out just anterior to the liver.

There is no external difference in the structure of the animals such as would enable one at a glance to differentiate male from female. It was thought that there might be some difference in shell-form in the two sexes—for example, the relation between diameter and height—but after some hundreds of shells had been measured and examined it was found that no such difference exists. The normal method of ascertaining the sex is to break the apex of the shell and examine the gonad. In mature or nearly mature animals thus broken the sex can be told at once, males having a white or creamy-white gonad, whereas in females it is green to dark green. In immature animals the sexes cannot be distinguished by eye. This method of breaking the shells is wasteful, as all animals so treated soon die.

3. HABITAT.

Trochus on Low Isles occurs in great numbers on those edges of the reef that are open to the direct action of the dominant South-east seas. From the map of Low Isles it will be seen that, owing to the peculiar arrowhead shape of the island, the influence of these seas is felt over that portion of the island commencing at the north-east spit, passing through the east and south, and extending to the south-west corner. A few animals are to be found on the other edges, the moats, and the reef-flat, but they are not present in sufficient numbers in these places to warrant their being fished.

In general, the animals occur on the weather side of reefs, but where the reefs are narrow they are more or less evenly distributed. They shun, however, the sandy and the "grassy" localities.

It was found in attempting to keep these animals in captivity that they require the highest possible conditions of aëration, together with an abundance of food. These conditions, and also the absence of mud and silt, obtain on the weather side of reefs, so that these areas are the ideal home for *Trochus*.

On the boulders along the reef-edges rich growths of algae occur, and it is upon these plants that *Trochus* feeds. The small plants are rasped off the rocks and shingle by means of the many-toothed radula, and the scraped-off food is drawn into the mouth, sand-grains, together with foraminifera and other small animals, being also swallowed.

Trochus is a littoral animal, though an occasional example has been found in deep water. The greatest recorded depth is that of 12 fathoms, given in the "Challenger" Report (Watson, 1886), but it is not stated whether the specimen was living when found. Traverses were run out into deep water at Low Isles, and not one *Trochus* was found in, or reported from, water more than 3 ft. deep at lowest springs. The majority occur between the level of high-water neaps and the lowest springs mark. It is therefore quite common to find these animals exposed by the tide, though some are never out of water.

There appears to be a certain zoning of the animals. At the high-neaps mark on the shingle beach the smallest forms are found, those up to 2 cm. in diameter being commonest. These are generally found in, or close to, runnels formed by the water from the moat escaping through the shingle. In these runnels algae are very common, so food is plentiful. Next are found the 3 and 4 cm. animals, in such a position that they are bared by moderately low tides. Then come slightly larger forms, dominant amongst them being the 5 and 6 cm. ones; and lastly come the largest animals, these being bared only by the lowest springs. The absence of large forms from Low Isles reef is due to the continuous fishing by the *Trochus* hunters.

Despite this general statement there is frequently to be found a mixing of forms at the lowest springs mark, for, in suitable spots, such as that presented by a large flat slab or gnarled boulder, animals ranging from 2 to 9 cm. in diameter have been observed.

Trochus is gregarious, the main reasons for the animals gathering together being the presence of abundant food and ample hiding spaces in and under the boulders. On several occasions as many as 15 animals were taken from one slab or boulder. Generally the size of the animals in these communities is remarkably uniform, though there are exceptions.

At low water those animals left high and dry on the shore are exposed for some hours. In these circumstances they creep into crevices in the boulders or hide below them. For many hours they can survive thus; in fact, *Trochus* kept out of water but in the shade for two days completely revived after being returned to the sea.

When covered by the sea *Trochus* scatters over the shingle and boulders. Feeding appears to proceed at every opportunity, so that the amount of faecal matter deposited is very great. This faecal track has often been the means of tracing an animal that was otherwise hidden.

In order to see whether *Trochus* is sedentary or given to wandering, 80 animals, ranging in diameter from 2 to 5 cm., were file-marked, numbered and instantly liberated at the spot from which they were taken. Each was measured in order to keep a record of actual growth. In the first month 53 were present, for the second month 27 were found, and for the third only 21 were seen. Many immigrants were found to have arrived, showing that there was sufficient food to maintain the original inhabitants had they stayed.

It would appear from this experiment that the animals move freely about the reef. Some of the animals had moved as much as 50 yards from the original rocks, but this distance has frequently been exceeded in one night by specimens placed in a small lagoon close to the island in readiness for examination next morning.

4. GROWTH RATE AND AGE.

In order to find the rate of growth of *Trochus* the following methods were adopted :

- (1) The measurement of marked and numbered animals confined in cages.
- (2) The monthly measurement of some 600 free-living animals found on the south-east edge.
- (3) The measurement of specially marked animals living freely on the south-east edge.

The first experiment was commenced in the last days of July, 1928. Two enclosures of wire-netting were constructed in a runnel from the western moat. The shape of the cages was roughly hexagonal, with sides of approximately 6 yards. In one of these enclosures 90 animals of various sizes were placed, while in the other 50 small animals were imprisoned.

Each month these animals were measured, and at the same time fresh alga-coated rocks were supplied. In October 60 of the larger and 44 of the smaller were present. A dwindling in November was followed by the almost complete destruction of the animals in December, only 1 small and 8 large specimens being found, though many broken shells were collected. Sting-rays, which made their appearance on the reef-flat in large numbers about this time and had been observed in the enclosures, hermit crabs, especially the red *Dardanus megistos*, and whelks, were without doubt responsible for much of the havoc, though a small percentage of the *Trochus* escaped over the walls of the enclosures.

Each shell was file-marked, the mark being placed on the whorl directly above the mouth of the shell. At the time of measuring and marking each shell was numbered. It was found that lead-pencil marks, if placed on the nacreous layer within the shell-mouth, would stand for a considerable time, so this means of numbering each shell was adopted. This number was soon hidden, for the growth of the shell shifted the aperture, therefore at each measurement the number was renewed.

In measuring the shell the greatest diameter was adopted as standard. This was obtained by placing the shell between the jaws of sliding vernier calipers, and measuring the base of the shell from the aperture over the columella to the opposite side.

A list of these measurements is here given, from which it will be seen that the average increase for the four months, from July to November, was approximately 2 mm. per month.

After the failure of this growth-rate experiment it was decided to commence a new series of experiments, and the measurement of approximately 600 free-living animals found on the south-east reef-edge was carried out in December and each month thereafter, the final reading being taken in July.

These animals were merely measured, and then replaced as nearly as was practicable in the place from which they had been taken. In order to avoid measuring the same animal twice, the inside of the mouth of each shell was scored with pencil at the time of

measuring. This mark, besides preventing the duplicating of readings in any month, gave the information that that animal had been seen the previous month.

The ground covered in this experiment was about 500 yards in length, and the same area was always worked over each month.

The results of these measurements are given in Table III. The measurements were divided into groups with a difference of 0·20 cm. For example, all those diameters between 2·21 and 2·40 cm. inclusive were placed in the one group known as the 2·40 group. Since the number measured each month varied, although it was never less than 600, percentage frequency has been given.

TABLE I.—*Larger Forms. Showing Monthly Measurements of Greatest Diameter and Total Increase (in centimetres) after Four Months.*

No.	July.	August.	September.	October.	November.	Increase.
1	2·92	3·09	3·40	3·69	3·97	1·05
2	3·12	3·22	3·50	3·71	3·96	·84
3	3·00	..	3·60	..	3·96	·96
4	3·20	3·27	3·55	3·85	4·05	·85
5	3·28	3·39	3·41	3·64	3·95	·67
6	3·47	3·65	3·85	4·07	4·22	·75
7	3·51	3·64	3·83	4·14	4·40	·89
8	3·51	3·74	4·00	4·20	4·45	·94
9	3·54	3·69	3·95	3·97	3·99	·45
10	3·62	3·69	3·98	4·25	4·33	·71
11	3·66	3·77	4·05	4·24	4·44	·78
12	3·73	3·82	4·05	4·23	4·50	·77
13	3·73	3·89	4·05	..	4·42	·69
14	3·73	3·85	4·12	4·37	4·51	·78
15	3·75	3·82	4·09	4·37	4·67	·92
16	3·77	3·80	4·00	4·19	4·43	·66
17	3·78	3·90	4·05	..	4·60	·82
18	3·84	3·96	4·10	4·40	4·59	·75
19	3·87	3·91	4·34	4·57	4·75	·88
20	4·04	4·10	4·34	4·63	4·83	·79
21	4·08	4·16	4·46	4·76	4·90	·82
22	4·10	4·20	4·44	4·68	4·87	·77
23	4·10	4·21	4·47	4·68	4·94	·84
24	4·11	4·16	4·35	4·53	4·59	·48
25	4·17	4·22	4·44	4·65	4·85	·68
26	4·22	4·28	4·52	4·74	4·92	·70
27	4·28	4·40	4·56	4·85	5·10	·82
28	4·35	4·38	4·59	4·79	4·92	·57
29	4·39	4·46	4·76	4·84	4·87	·48
30	4·41	4·50	4·74	5·00	5·13	·72
31	4·41	4·55	4·75	5·02	5·20	·79
32	4·45	4·52	4·71	4·98	5·17	·72
33	4·48	4·55	4·69	4·87	5·02	·54
34	4·64	4·72	4·91	5·08	5·18	·54
35	4·65	4·75	4·95	5·09	5·23	·58
36	4·66	4·72	..	5·02	5·05	·39
37	4·75	4·88	5·05	5·07	5·20	·45
38	7·96	8·02	8·08	8·11	8·18	·22
39	8·30	8·33	8·34	8·34	8·34	·04

TABLE II.—*Small Forms. Monthly Measurements of Greatest Diameter and Total Increase (in centimetres) after Three Months.*

No.	August.	September.	October.	November.	Increase.
1	4.67	4.67	4.77	4.98	.31
2	4.25	4.47	4.78	5.00	.75
3	3.74	4.03	4.24	4.43	.69
4	3.68	3.92	4.25	4.50	.82
5	3.36	3.50	3.82	4.04	.68
6	3.28	3.30	3.36	3.67	.39
7	2.92	2.95	3.13	3.42	.50
8	2.81	3.00	3.39	3.60	.69
9	2.89	2.95	3.21	3.23	.34
10	2.84	2.89	3.10	3.28	.44
11	2.83	3.00	3.11	3.24	.41
12	2.81	2.95	3.16	3.41	.60
13	2.80	..	2.96	3.13	.33
14	2.61	2.62	2.80	3.09	.48
15	2.60	2.68	2.80	3.15	.55
16	2.60	2.70	2.87	2.88	.28
17	2.56	2.64	2.80	2.99	.43
18	2.53	2.69	3.01	3.22	.69
19	2.53	2.58	2.82	3.04	.51
20	2.52	2.52	2.78	2.97	.45
21	2.52	2.66	2.87	3.21	.69
22	2.51	2.60	2.82	3.07	.56
23	2.50	2.47	2.68	2.94	.44
24	2.47	2.48	2.61	3.03	.56
25	2.47	2.52	2.84	3.12	.65
26	2.42	2.42	2.56	2.76	.34
27	2.36	2.42	2.64	2.89	.53
28	2.33	2.39	2.53	2.83	.50
29	2.19	2.20	2.43	2.66	.47
30	2.17	2.20	2.53	2.87	.70
31	2.08	2.08	2.22	2.50	.42
32	2.06	2.22	2.48	2.71	.65
33	2.05	2.12	2.44	2.64	.59
34	2.04	2.07	2.30	2.50	.51
35	2.01	2.17	2.36	2.48	.47
36	1.93	2.01	2.21	2.53	.60
37	1.97	2.03	2.14	2.50	.53
38	1.94	2.00	2.22	2.42	.48
39	1.80	..	2.08	2.32	.52

The drawing of conclusions from these figures is hindered by the fact that regular fishing of the larger forms took place during the term of the Expedition on Low Isles. Old and large forms are therefore missing. However, it will be seen that :

(1) The mode moved from about 4 cm. in January to 5.4 cm. in July. That is, the growth was approximately 1.4 cm. in six months.

(2) There was an anomalous result for June, the figures being irregular, with apparently several modes. This is probably due to the fact that *Trochus* tends to hibernate during the cold months of the year, so that many escaped detection by remaining beneath the boulders and a representative sample was thus not obtained.

(3) There is a marked absence of very young and of very old animals. The young are most difficult to detect, as their colours blend so remarkably with those of the Lithothamnion-covered shingle. The smallest had a diameter of 1.47 cm. The older forms, as stated earlier, are regularly fished.

(4) The preponderance of 4 to 5 cm. animals in March points to there having been an extremely good fall of spat in 1927, with the subsequent survival of a large proportion of the individuals.

The third method of measuring growth was begun in January, 1929, after the failure of the first method. In this experiment free-living animals on the south-east edge were used. The animals were file-marked and numbered at the time of their measurement. The work was severely handicapped, because at first only night tides could be worked, and then the beginning of the wet season added to the discomforts.

One hundred and two animals, varying in diameter from 2 to 5 cm., were chosen. As soon as they were marked and measured they were placed back on or under the block where they were found. Each block was marked by a stake for future identification, but no fencing of any kind was constructed, so that the animals were free to wander.

TABLE III.—*Results of Measurements of some 600 Free-living Trochus given as Percentage Frequencies.*

Group.	Percentage frequency.							
	December.	January.	February.	March.	April.	May.	June.	July.
2.00 cm.	..	..	..	..	..	..	.1	..
2.20 "	..	..	..	.2	..	..	.1	.1
2.40 "	..	..	1.1	.3	..	..	.1	.3
2.60 "	..	.2	..	.9	1.5	.5	.1	.5
2.80 "	..	.5	.8	.5	3.0	1.3	.1	.9
3.00 "	..	2.1	1.3	2.0	4.3	2.6	1.1	.7
3.20 "	..	4.8	2.5	2.7	3.1	4.9	2.1	.5
3.40 "	..	11.5	4.5	2.0	2.6	4.8	2.9	1.7
3.60 "	..	16.1	5.8	4.2	4.7	3.2	3.2	2.1
3.80 "	..	13.5	7.8	5.5	6.5	2.6	4.5	2.1
4.00 "	..	10.9	13.2	9.3	6.0	3.6	2.9	3.3
4.20 "	..	9.3	9.2	13.3	8.1	6.0	4.8	4.0
4.40 "	..	5.8	7.3	16.0	10.1	5.5	5.0	4.4
4.60 "	..	3.7	6.8	12.6	9.6	6.6	6.7	5.2
4.80 "	..	1.8	2.5	6.9	9.3	9.5	7.1	5.5
5.00 "	..	2.4	2.5	5.2	6.1	11.1	10.0	6.8
5.20 "	..	2.4	3.5	2.5	6.5	10.1	9.5	9.4
5.40 "	..	2.4	3.6	2.0	3.1	7.8	9.7	10.9
5.60 "	..	2.9	4.5	1.6	1.8	6.5	8.3	10.3
5.80 "	..	1.3	5.6	2.5	1.1	4.8	7.3	9.6
6.00 "	..	2.6	5.4	2.5	2.1	1.9	6.1	9.4
6.20 "	..	1.5	4.0	1.1	1.0	1.0	2.6	4.8
6.40 "	..	1.0	4.1	2.2	1.3	1.1	2.1	3.2
6.60 "	..	.2	2.8	1.3	3.5	1.1	1.0	1.4
6.80 "	..	.2	1.8	1.1	1.6	.8	1.0	.3
7.00 "	..	1.0	.8	.6	2.0	.6	.5	.6
7.20 "	..	.2	..	.2	.6	1.0	.1	.6
7.40 "	..	.2	..	.2	.1	.8	.5	.1
7.60 "	..	.5	..	..	..	.3	.3	.6
7.80 "	..	.8	..	..	..	.1	.1	.4

TABLE IV.—*Monthly Measurements of Free-living Trochus and Total Increase after Six Months (in Centimetres).*

No.	January.	February.	March.	April.	May.	June.	July.	Increase.
1	2.00	2.57	3.01	..	..	..	3.95	1.95
2	2.12	2.56	2.95	3.33	..	..	3.73	1.61
3	2.60	3.20	..	..	..	4.57	4.63	2.03
4	2.62	3.15	3.44	3.81	..	4.31	4.37	1.75
5	2.66	..	3.61	3.93	..	4.50	4.57	1.91
6	2.75	3.25	3.64	4.00	..	4.57	4.63	1.88
7	2.91	3.30	3.57	3.87	..	4.42	4.54	1.63
8	2.91	3.37	4.20	..	..	4.60	4.81	1.90
9	3.05	3.65	4.04	4.41	..	4.70	4.97	1.92
10	3.07	3.60	3.98	4.44	..	4.93	5.00	1.93
11	3.10	..	4.12	4.49	..	5.02	5.06	1.96
12	3.13	3.56	3.75	..	..	4.28	4.40	1.27
13	3.20	..	3.92	..	..	4.51	4.63	1.43
14	3.26	..	4.29	..	..	5.21	5.32	2.06
15	3.45	4.03	4.37	4.66	..	5.18	5.27	1.82
16	3.57	4.09	4.43	4.75	..	5.20	5.20	1.63
17	3.60	4.14	4.32	..	..	4.90	5.06	1.46
18	3.61	4.14	4.53	4.86	..	5.32	5.43	1.82
19	3.64	4.12	4.48	4.75	..	..	5.46	1.82
20	3.67	4.24	..	..	..	5.32	5.42	1.75
21	3.70	4.30	4.60	4.91	..	5.56	5.68	1.98
22	3.74	4.00	4.41	4.66	..	..	5.25	1.51
23	3.76	4.42	4.70	5.11	..	5.76	5.81	2.05
24	3.91	4.31	4.60	5.00	..	5.42	5.47	1.56
25	3.94	4.34	4.60	5.05	..	5.57	5.64	1.70
26	3.96	4.25	4.43	..	..	4.94	5.01	1.05
27	3.97	..	4.62	4.87	..	5.16	5.17	1.20
28	3.97	4.33	4.76	..	..	5.26	5.27	1.30
29	4.09	..	..	..	..	6.10	6.20	2.11
30	4.13	4.57	..	..	..	4.68	4.71	.58
31	4.46	4.83	..	..	..	5.33	5.39	0.93

Total Increase after Five Months.

32	2.32	2.72	3.02	..	..	3.70	..	1.38
33	3.02	3.58	3.78	4.20	..	4.72	..	1.70
34	3.31	4.04	4.41	4.65	..	5.15	..	1.84
35	4.34	4.72	5.02	5.37	..	5.72	..	1.38

Total Increase after Four Months.

36	..	2.72	2.99	3.25	..	3.72	..	1.00
37	..	3.44	..	..	..	4.97	..	1.53
38	..	4.61	..	5.17	..	5.55	..	0.94

Total Increase after Five Months.

39	..	2.26	2.56	2.92	..	3.40	3.47	1.21
40	..	2.75	..	..	..	..	3.60	0.85
41	..	2.77	..	3.21	..	..	3.80	1.03
42	..	2.83	..	..	..	..	3.88	1.05
43	..	3.17	..	..	..	..	4.22	1.05
44	..	3.32	3.67	4.02	..	4.65	4.82	1.50
45	..	3.73	4.05	4.49	..	5.11	5.24	1.51
46	..	3.86	4.25	..	..	..	5.14	1.28
47	..	3.99	4.32	4.55	..	5.05	5.11	1.12
48	..	4.11	4.36	..	..	..	4.82	0.71
49	..	4.19	4.58	4.98	..	5.43	5.51	1.32
50	..	4.52	..	..	..	5.65	5.77	1.25

Each month, except May, as many as could be found were measured and the results listed. On July 22nd the final measurement was made, and only 43 of the original 102 animals were discovered. Twenty of them had disappeared at the first reading, so 20 immigrants were added to the number under observation. Twenty-nine seen on only one occasion after being marked and 23 seen twice have been excluded from the results as they are of no consequence.

Growth is very irregular, and animals of approximately the same diameter at the beginning of the experiment were found to differ frequently by as much as 0.5 cm. at the end of six months. This irregularity in growth will probably explain the irregularities in Table III, which shows the measurement of approximately 600 *Trochus*.

In Table IV the measurements of the animals in this experiment are given. Though great variations in growth-rate exist, it appears safe to assume that animals one year old are from 2.5 to 3 cm. in diameter, two years old are 5 to 6 cm., three years, 7 to 8 cm. Above this size, owing to the definite flattening out of the whorls, growth is probably very slow, but as few animals of large size were found, no age can be given for them. The writer cannot, however, agree with Hedley's statement that *Trochus* six months old are 2 in. (5 cm.) in diameter, and one year old are 3 in.

From these figures there is seen to be a definite slackening off in the amount of shell deposited by the animals during the colder months, and in one or two cases there has been a complete cessation in shell-deposition. This period is not only one of rest from shell-building; it can be termed a time of hibernating, for most *Trochus* feed but little and remain hidden below the boulders.

5. REPRODUCTION.

The sexes in *Trochus* are separate, and there is no external sexual difference. The method by which the sex can be determined is described on p. 146.

Weekly gonad samples were taken, using *Trochus* varying in diameter from 3 to 9 cm., and in all 400 animals were examined. Of 300 of these, 147 were males and 153 females. The remaining 100 were small forms ranging from 3 to 5 cm., used in order to find at what age the animals matured. These were all found to be immature, but many of the larger ones were so far advanced as to allow of their sex being readily determined. The result of this work points to the sexes being present in equal numbers, and to the fact that animals smaller than 5 cm. are, in general, immature.

The method of examining the gonad proved very wasteful, for the animals with the apex of their shell removed were open to the attacks of other animals and they soon died. Owing to these deaths, experiments on sex-change could not be carried out, so that the close examination of all gonadal products was adopted. In no case were sperm and eggs found together, though many instances of large eggs undergoing resorption mixed with small, developing eggs were found. This points to there being no change of sex in moderately young *Trochus*, but the matter requires further examination.

Many attempts to keep *Trochus* in captivity in an aquarium were made, but in every instance the animals soon showed signs of distress, and many valuable spawning animals were lost through persisting with this attempt. In order to hold these animals in captivity it was found necessary to place them in jars left out in the sea. There soon developed within the pots a strong growth of filamentous algae (*Enteromorpha* sp.), and on this growth the animals thrived. Many *Trochus* so imprisoned in March were in good health in July.

The animals were visited daily, and on 22nd March, just as the flooding tide covered the jars, one animal was found extruding eggs. The temperature of the water was 28.2° C. The eggs are freed into the water and then float away, but in the still water within the jars they soon settled, floating again at the slightest stirring of the water.

The eggs of this specimen, as of others found later, were freed through the exhalant siphon as the foot was retracted. They were liberated a few at a time, and in no case were great clouds of eggs seen. *Trochus*, therefore, differs in this respect from *Haliotis* (Stephenson, 1924).

The laying operation appears to be protracted. One female first observed extruding eggs in June was still laying freely in late July. This animal was preserved, and on breaking the shell the ovary was seen to contain enormous numbers of eggs that readily washed free.

Only two males were actually observed extruding their products. The sperm was liberated in such quantities as to cause a cloudiness in the water caught up in the mouth of the shell, though there was no noticeable milkiness in the surrounding water.

Trochus appears, therefore, to be a winter-breeder, the season extending from March to July at least, and each animal possesses a protracted spawning period.

The eggs of *Trochus* at, and just before, extrusion are spherical. Before they are perfectly mature they are of irregular shape, owing to mutual pressure. Those taken from the ovary are each encased in three egg-cases. The outer one is regularly pitted, and gives to the egg a total diameter of 0.5 mm. Within the outer case is a second one, which becomes much more apparent in stale eggs as a cloudy coating. Next comes a transparent coat, which is clearly marked off from the other two, even in fresh specimens. In immature eggs the nucleus is easily discernible, but in mature ones the abundance of green yolk hides it.

The naturally extruded egg differs from those taken from the ovary in that the two outer cases are absent. The extruded egg (chorion included) has a diameter of 0.3 mm., of which the egg proper is 0.17 to 0.25 mm.

The sperm consists of a cylindrical head, rounded anteriorly and indented posteriorly, and a long flagellum. The head of the sperm is 0.007 mm. long, and the tail is approximately five times as long as the head.

Artificial fertilizations, using the naturally extruded eggs and sperm, were effected. In four hours after mixing the products the first division had commenced. Division was equal. The stages following the first division were not observed, but in twenty hours after mixing many of the egg-cases contained ciliated embryos, the rapidly beating cilia causing the embryo to rotate slowly within the case. At this stage the experiment was left, and on returning to it later it was found that the young had completely vanished, many ciliates present in the bowls being probably responsible for the loss. No success attended many further attempts at fertilization.

An earlier worker on *Trochus*, Montague, who died before completing his experiments, was of the opinion (1915) that *Trochus* were not mature until they had reached a basal diameter of 8.5 cm. This would make these animals about three years old. The first animal that the writer observed extruding eggs was 7.83 cm. in base. From this moment all *Trochus* found on the reef were closely examined, particular attention being paid to those animals of 4 to 5 cm. base. Amongst the many found laying there were, in particular, those of the following diameters: 4.40, 4.80, 5.05, 5.80, 6.08 and 6.30 cm. amongst

the females, and 5.61 and 7.22 amongst the males. The 4.40 animal was found in the moat, where conditions for normal growth are not favourable, so that this specimen can be regarded as one of retarded growth.

Trochus seems, therefore, to become mature at two years old, that is, when the shell is in general 2 to 2.5 in. in basal diameter.

6. SUMMARY.

1. *Trochus* is a "scraping" gastropod.
2. It is essentially a littoral animal and can withstand protracted periods out of water.
3. There is a tendency towards zoning, the oldest animals being found at or about lowest springs mark.
4. Shell-growth is continuous, though there is a slackening off of shell-deposition during the winter months.
5. There was a marked absence of young forms from Low Isles.
6. The animals seem to roam fairly widely in search of food.
7. Animals of base 2.5 to 3 cm. are considered one year old, those of 5 to 6 cm. are two years old, and those of 7 to 8 cm. are three years old.
8. The sexes are present in equal proportions.
9. Though the smallest *Trochus* found laying eggs was 4.40 cm. in diameter, they are not, in general, mature until two years old.
10. The eggs are spherical, and are freed into the water a few at a time. The laying season certainly extends from March till July; it is probably much more protracted.
11. Successful artificial fertilizations were carried out, though all stages in the development were not observed.

7. REFERENCES.

- HEDLEY, C. 1917. The Ecomonics of *Trochus niloticus*. Aust. Zool., Sydney, I, pp. 69-73, pls. v, vi.
- MONTAGUE, P. D. 1915. Notes on *Trochus niloticus*. Agricultural Review of New Caledonia, No. 45, pp. 39-43.
- RANGLES, W. B. 1904. Some Observations on the Anatomy and Affinities of the Trochidae. Quart. J. Micr. Sci. XLVIII, pp. 33-78, pls. iv-vi.
- ROBERT, A. [1899-] 1900. Le Troque: L. Boutan in "Zoologie descriptive," II, pp. 381-415, text-figs. 493-508.
- STEPHENSON, T. A. 1924. Notes on *Haliotis tuberculata* I. J. Mar. Biol. Ass. U.K. XIII, pp. 480-495, text-figs. 1, 2.
- WATSON, R. B. 1886. Report on the Scaphopoda and Gasteropoda collected by H.M.S. "Challenger" during the Years 1873-76. "Challenger" Reports, Zoology, XV, pp. v + 756, pls. i-liii, text illust.
- YONGE, C. M. 1928. Feeding Mechanisms in the Invertebrates. Biol. Rev. Cambridge, III, pp. 21-76, text-figs. 1-25

ON THE GROWTH OF THE ADULT COLONY OF POCILLOPORA BULBOSA

BY

S. M. MANTON, M.A., PH.D.

*Demonstrator in Comparative Anatomy in the University of Cambridge,
and Fellow of Girton College*

WITH FOUR TEXT-FIGURES AND ONE PLATE

INTRODUCTION.

THE object of this investigation, which was started at the suggestion of Prof. Stephenson, was to observe in detail the method of growth of a mature colony of *Pocillopora* for comparison with the early development of the same form worked out by Prof. Stephenson. It was originally intended to study in particular the method of formation and growth of the new polyps by keeping living colonies under constant observation. Twelve small colonies of *Pocillopora bulbosa* were attached to concrete blocks 3 in. square, and the latter were fastened by wires to the inner walls of an open tub situated in the Western Moat (the natural habitat of the species) and always submerged. It was found, however, that growth was so rapid that it would have been necessary to examine the colonies at least every three days in order to follow the growth of individual polyps. Time did not permit of an examination being made more frequently than once a fortnight, and hence a record of the growth changes from month to month only is recorded, together with the observation of many isolated stages in polyp formation. Subsequent examination of part of the corallum of a colony whose growth stages had been followed proved of interest, as the relative ages of most of the corallites was known, and the relation between soft tissue bearing polyp buds in process of formation and the hard parts below could be ascertained.

PREVIOUS WORK.

The growth of entire coral colonies over periods of months and years has been investigated most recently by Mayor (1924) and Stephenson (to be published shortly in this volume). Mayor summarizes the previous published work on the subject, and records the increase in linear dimensions and in weight of *Pocillopora damicornis* var. *cespitosa*, *P. eydouxi* and *P. brevicornis* (1924, pp. 62, 66-67, and 71-72). Respecting the genus *Pocillopora* Gardiner remarks that, "The growth of the colony is much more vigorous towards the summits of the branches, and to this is due the angular character of the calices here and their very thin walls" (1897, p. 942). Increase in the number of corallites takes place

by gemmation, fissiparity being very rare (Duncan, 1885, p. 47). Accounts of the main types of development of the corallum in the Madreporaria are given by Ortmann (1890), von Koch (1896) and others, and multiplication of the soft parts has more recently been studied by Duerden (1902, 1903, etc.) and Matthai (1926), but none of these accounts deal with the Pocilloporidae. Many photographs and figures of the Pocilloporidae have been published, but they do not show the skeletal details of budding (Hoffmeister, 1925; Vaughan, 1907 and 1918; Dana, 1846, etc.), and the process is very briefly described by Milne Edwards (1860, p. 302). The present account gives for the first time details derived from a study of the living and growing colony.

GROWTH AND BUDDING OF POCILLOPORA.

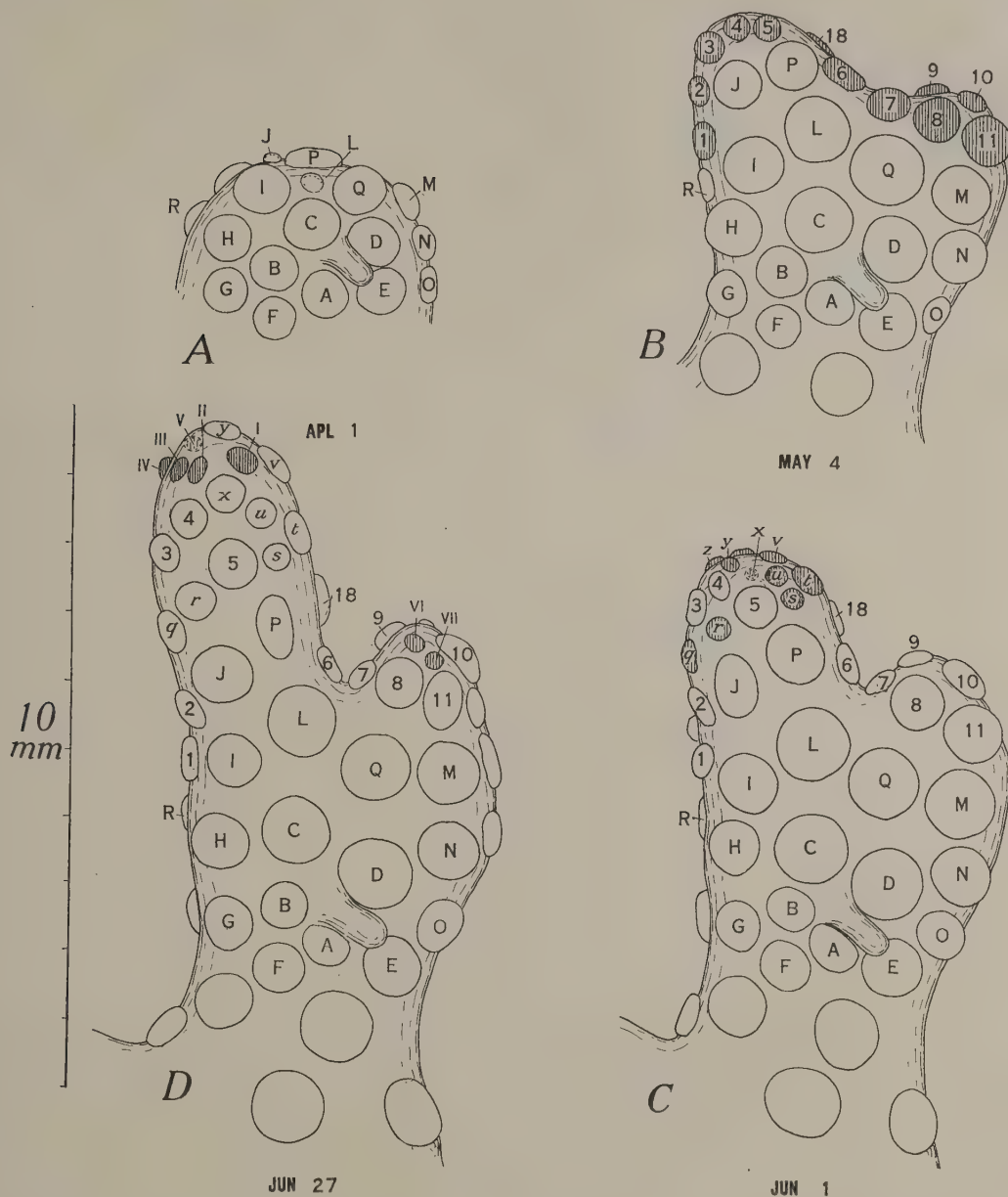
Text-figs. 1 and 2 record the changes undergone by the terminal portion of a branch on an actively growing colony of *Pocillopora bulbosa*. The dimensions of the colony were about 5×3.5 cm. and 2.5 cm. high. At the side of one branch, 2 mm. from the tip on 1st April, a solid knob-like outgrowth projected bearing no polyps, and this abnormality served as a recognizable fixed point of reference for subsequent growth. The diagrams in Text-fig. 1 show the positions of the polyps on the branch in side view, new polyps formed during the previous month being cross-hatched. When viewed from above on 1st April the branch appeared as indicated in Text-fig. 2, *A*. The polyps were moderately expanded in diffuse light; in strong sunlight they contracted within the calix.* In mature polyps the twelve tentacles are of almost equal length. Mesenteries were not always clearly visible through the tissues.

By 4th May considerable growth had taken place, and when the same branch was viewed from above, few of the original polyps were visible (see Text-fig. 2, *C* and *D*), and the projecting knob was no longer apparent from above. From Text-figs. 1, *A* and *B*, and 2, *A-D* it will be seen that the increase in height above the knob from 2 mm. on 1st April to 4.8 mm. on 4th May has been accomplished by (1) the addition of new polyps situated in between the old ones at the tip (in Text-fig. 1, *D*, old polyps are marked **A**, **B**, **C**, etc., new polyps **1**, **2**, **3**, etc.), and (2) by the spreading out and divergence of the polyps already present. The branch had also widened considerably at the tip and showed signs of becoming bifid, a furrow extending across it (Text-fig. 2, *C*).

After another month's growth the branch became definitely bifid, but one branchlet was much longer than the other, and bore numerous new apical polyps (Text-fig. 1, *C*, *q*, *r*, *s*, etc., cross-hatched). The second branchlet had been formed mainly by upward and outward growth of the original corallites, only one new polyp appearing at the apex, and not visible in side view (Text-fig. 1, *C*). Growth of the lower polyps had continued to a slight extent, polyps **L** and **Q**, etc., being further from the knob. The tip of the longer branchlet now measured 6.2 mm. from the knob.

By 27th June the longer branchlet extended 8 mm. beyond the knob and had increased greatly in size by both the above-mentioned methods, the new polyps lying in between the old ones at the tip (Text-fig. 1, *D*, and 4, *A*, **I**, **II**, **III**, etc., hatched). The shorter branchlet had grown slightly and showed three new apical polyps. The main axis of the branch below the bifurcation had not elongated, and polyps **L**, **Q**, etc., remained at the same distance from the knob and from each other.

* This applies to certain colonies of *Pocillopora* only; many will expand their polyps in full sunlight.



TEXT-FIG. 1, A-D.—Diagrams of the side view of a growing branch of *Pocillopora bulbosa*, showing the size of the branch and the positions of the polyps present on 1st April, 4th May, 1st June and 27th June respectively. Polyps appearing for the first time during the previous month are cross-hatched. Polyps of different ages are numbered or lettered as follows:

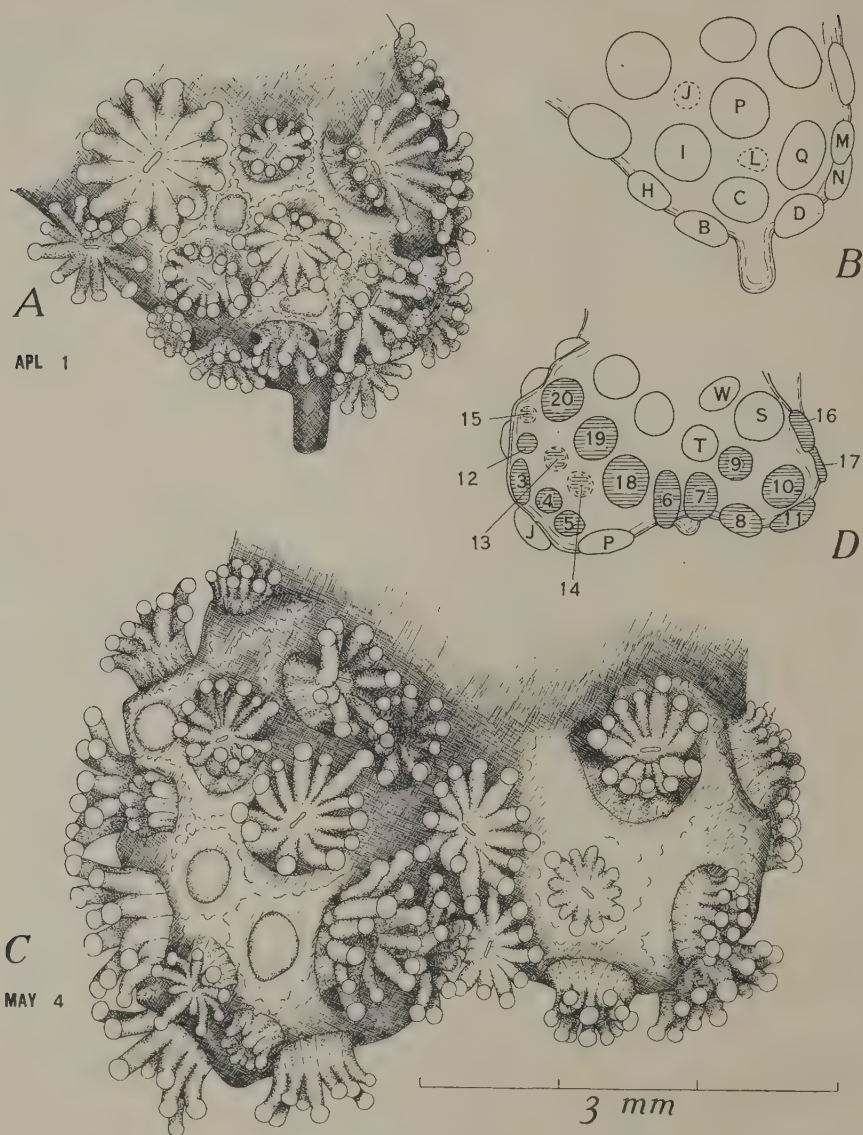
A, B, C, etc., polyps present on 1st April.

1, 2, 3, etc., new polyps formed between 1st April and 4th May.

a, b, c, etc., new polyps formed between 1st April and May 4th.

i, ii, iii, etc., new polyps formed between 1st June and 27th June.

The abnormal knob-like outgrowth which served as a fixed point for observing growth is seen in Text-figs 1, A-D.



TEXT-FIG. 2, *A* and *C*, show the appearance of the same living branch of *Pocillopora* when viewed from above on 1st April and 4th May respectively. The abnormal knob-like projection which served as a fixed point for observing subsequent growth is seen in Text-fig. 2, *A*. TEXT-FIG. 2, *B* and *D*, give a key to the lettering and numbering of the polyps seen from above on those dates; the diagrams are on the same scale as the side views of the branch seen in Text-fig. 1, *A* and *B*. The lettering and numbering is the same as for Text-fig. 1, where a key is given. For further description reference may be made to the text.

In 88 days the linear increase of the branch above the knob was approximately 6 mm., but very little increase in height occurred below it. Active growth in length is limited to the tips of the branches of the colony, but growth in thickness takes place everywhere. The growth rate of the branch under observation corresponds to an annual increase in height of 25 mm. Mayor records an increase of 7–28.5 mm. per annum for *Pocillopora damicornis* var. *cespitosa* in Pago Pago Harbour, and 37–61 mm. on the Aua line in Samoa. Thus it may be assumed that the colony under observation on Low Isles was healthy and growing at a normally rapid rate. It may be noticed that the linear growth-rate was not constant during the three months of observation, the increase per day being on an average 0.101 mm., 0.092 mm. and 0.069 mm. during the months of April, May and June respectively. The surface temperature of the sea during these three months gradually fell about 6.5° C., from 27.4° C. to 21° C. It is not clear from the insufficient data available whether the observed fall in growth-rate bears a direct and simple relationship to the fall of temperature, since it is possible that besides being influenced directly by temperature, a branch at different ages may normally grow at various rates.

FORMATION OF NEW POLYPS.

It has been seen that the formation of new polyps was restricted to the apex of the branch figured. On the entire colony polyp-formation occurs most rapidly at branch tips, and on the edge zone of the encrusting basal part of the colony. Some stages in the development of the soft parts of new polyps, as seen in surface view, are shown in Text-figs. 2 and 3. Polyps always arise by extra calicinal budding. The first indication of budding is seen in the appearance of a flat area of coenosarc between the existing polyps such as that lying between polyps 10, 16 and S in Text-fig. 2, C and D; three weeks later a fully-formed polyp occupied this situation. The corallum at such a stage already shows the beginning of the formation of the theca (see below). Budding may be much more rapid than this. For example, the space between polyps 5, 14, 18 and P seen in Text-fig. 2, C and D, gave rise to four fully-formed polyps during the following four weeks. The bud first appears externally as a convex circular area showing no external structure (Text-figs. 2 A and C, polyps J, L, 14 etc., 3, B and C). It then enlarges slightly, and pigmented stripes appear upon it corresponding in number with the tentacles and mesenteries. The stripes may alternate in size, and one larger than the rest may be formed at one side (Text-fig. 3, C). In other cases the pigmented stripes may be perfectly regular all round, and vary in number from about eight to twelve. Tentacles arise as bulges round the margin of the convex bud, and the mouth appears soon after tentacle formation has begun.

The details of tentacle formation here, unlike those in the very young colony (see Stephenson, 1931, p. 127), are very variable; but the adult polyps become almost similar, showing twelve sub-equal tentacles, or occasionally the directive tentacles slightly enlarged. The twelve tentacles may appear (1) almost simultaneously, or (2) the directive tentacles may arise first, followed by further tentacles appearing in couples, the directive tentacles remaining much larger than the rest for a considerable period. When twelve tentacles are formed together, large and small tentacles usually alternate, and the directive tentacles are not markedly larger than any other couple (Text-fig. 3, B, left-hand polyp, and 2, C, polyps 5, 12 and 9). Rarely eight or ten tentacles only may be formed together, but they similarly alternate in size; the polyps attain a large size

before the full number of tentacles is made up (Text-fig. 3, *B*, lower polyp). The dimorphism in tentacle size may be slight or very great, and persists till the polyp is nearly adult (Text-fig. 2, *C*, polyps 18, 19 and 20).

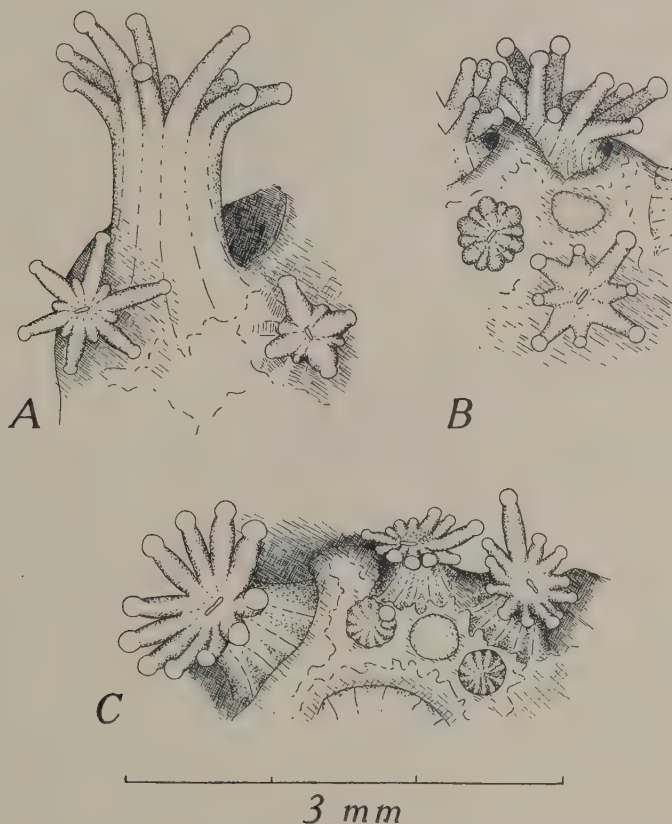
The colony shown in Text-fig. 3, *C*, shows one directive tentacle arising first and remaining much larger than the rest (two upper polyps), until the adult stage is reached (left-hand polyp), where the tentacles are practically equal. In such cases, where one or both directive tentacles arise first, they are followed either (1) by two large and three small couples, so that a regular alternation of large and small rudiments is formed (as in Text-fig. 3, *A*, left-hand polyp; the very young one on the right shows as yet the rudiments of one large and two small couples, besides the directive tentacles), or (2) by three large and two small couples. Where one directive tentacle is much larger than its fellow, the fifth (last) couple of tentacles to appear lies on either side of the second directive tentacle. Thus there is no constant order of tentacle formation in buds situated at the tips of branches, such as is seen in the early development of the entire colony, although the method apparent in adult colonies may be constant for the various parts of the same colony. A loss by the adult of the somewhat strict regularity of the early stages is a feature frequently met with in coelenterate development.

GROWTH OF THE CORALLUM.

After the colony had been examined on 27th June it was killed and the corallum cleaned (Plate I, fig. *A*). The history of all the apical corallites and of those over one side was known (see Text-fig. 1, *D* and 4, *A*). The youngest polyp rudiments visible externally in the soft tissue were *v* and *xii* (Text-fig. 1, *D* and 4, *A*). Polyp *v* had no mouth or tentacles, but pigmented stripes were present, and polyp *xii* appeared as a barely detectable convex area. Text-fig. 4, *B* shows a drawing from above of the skeleton at the tip of the longer left-hand branchlet; a satisfactory photograph of such a curved surface could not be obtained. Polyp *v*, although lacking mouth and tentacles, is provided with a small but definite calix, about 0.2 mm. deep (Text-fig. 4, *B*). The walls of the calix are slightly fluted and smooth and very thin, a narrow common calicinal wall separating the cavity of the calyx from those adjacent to it. Below the youngest visible polyp rudiment lies a concave platform *xii* appearing on a level with the upper edge of the calices of three adjacent corallites. In the soft tissues of the living colony no polyp rudiments were visible between polyps *v*, *x* and *ix*, or between *ii*, *x* and *y*, but the skeleton shows the initial stages of calix formation in these situations (Text-fig. 4, *B*, calices *xiii* and *xiv*).

The formation and growth of the calices in the adult *Pocillopora* appear to be as follows: At the tips of the branches the calices are crowded, so that there is a common narrow colline separating the cavities of adjacent calices. As the latter grow upwards and outwards in divergent directions, the free edge of the colline at the junction of two or three calices expands into a small flat area, as at *xiii* and *xiv* in Text-fig. 4, *B*. Shortly after this the polyp rudiment becomes visible externally, and growth of the edges of the calices converts the flat area into a concave hollow (Text-fig. 4, *A* and *B*, calix *xii*). Further growth of the colony results in the new calices becoming deeper, and at the same time wider as the older calices diverge from each other. Successive stages in this process are seen in calix *v* and in the slightly older calices *i*, *ix*, *x* and *xi* in Text-fig. 4, *B*, the latter being about 0.5 mm. deep, and less than three weeks old. The walls of these calices are now slightly

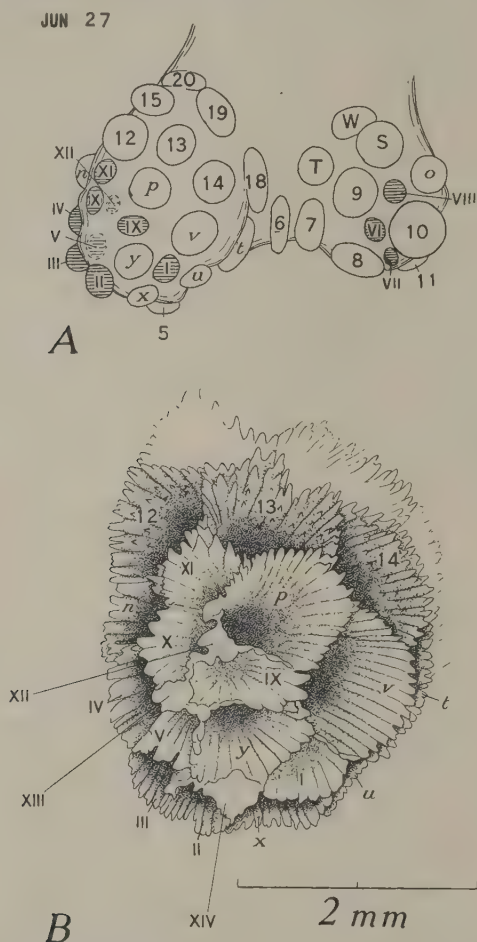
fluted, smooth and very thin. The surrounding calices *n*, *p*, *v* and *y* (Text-fig. 4, *B*, and 1, *D*) are older (less than six weeks), and are consequently deeper (1.2–1.5 mm.) and wider. Their cavities are V-shaped in section, with the bases very near together and lying below those of the younger polyps (Text-fig. 4, *B*); and they are united by a solid mass of skeleton formed by basal thickening of the calix walls. The collines are still sharp (Text-fig. 4, *B*, and Plate 1, figs. *A* and *B*, between calices VI and VII and between 8 and II), and the calix fluted and smooth within.



TEXT-FIG. 3, *A*, *B* and *C*.—Showing the appearance of portions of living *Pocillopora* colonies where growth is rapid and new polyps are being formed. For a description of the stages here shown, reference may be made to the text.

Calices 12, 13 and 14 (Text-fig. 4, *B*, see also Text-fig. 2, *D* and 4, *A*), are about ten weeks old. They are slightly larger than calices *n*, *p*, *y*, etc., and their cavities have the same maximum depth, although a thicker solid axis now lies between them. The walls have thickened so that one or two spines now lie on the free edge, and the twelve septa can be detected as twelve rows of spines within the calix. The direction of growth of the calix, however, has been turned towards the tip of the branch to a slight extent, and has been more rapid on the side nearer the tip, so that this side of the calix tends to overgrow the younger ones beyond it, and the deepest part of the calix lies immediately within its

proximal rim. The septa thus radiate in a fan-shaped manner over the distal wall from the deep basal part of the calix within its proximal rim, while the septa on the proximal wall are short, and hardly seen in direct surface view, as they lie within the rim (see photograph in Plate I, fig. *A*, calices 8 and 11).



TEXT-FIG. 4, *A*, shows diagrammatically the positions of the polyps, as seen from above on 27th June, on the branch of *Pocillopora* under observation, which is figured in side view on this date in Text-fig. 1, *D*. A key to the lettering is given with Text-fig. 1. This view of the branch may be compared directly with those shown in Text-fig. 2, *B* and *D* on 1st April and 4th May respectively. TEXT-FIG. 4, *B* shows part of the corallum at the tip of the left-hand fork of this branch (see also Plate I, *A*, side view). The lettering of the calices is the same as that of the polyps in Text-fig. 4, *A*. For further description of the formation of the calices and their subsequent development, as seen in this figure, reference may be made to the text.

Later the calices grow more slowly, and tend to do so directly outwards, so that the linear increase of the branch almost ceases. Growth in thickness of the branch continues by thickening of the walls and bases of the calices. The calices thus become further separated. This is clearly seen in Plate I, fig. *A*, where the sharp ridge between calices

8 and 11 bears one row of spines, that between Q and M three rows of spines, and that between D and O three to four irregular rows of spines. At the base of the branch as many as six rows of spines lie between two calices. With the outward growth of the calices the axial mass of skeleton increases and the calices become shallower. Their bottoms become flattened instead of V-shaped in section, and lie less than 0.5 mm. below the surface (Plate I, fig. A, calices C, D, etc.). The walls stand almost at right angles to the bottoms, and the septa are nearly radially symmetrical instead of showing the peculiar early symmetry noticed above. On the upper parts of the colony a columella is scarcely apparent and directive septa may just be detectable. On the basal encrusting portions of the colony a papilliform columella may rise from the base of the calix to the surface level. Its formation starts very early, as soon as the calix appears at the growing edge of the base of the colony.

Increase in thickness of the axial skeleton of the branches, resulting in the restriction of the calices to the outer parts of the corallum, is accomplished near the tips by deposition of solid skeleton at the bases of the calices, but elsewhere by the formation of tabulae. They are formed particularly rapidly in the angles between the branches and on the lower parts of the branches. Such an area is shown in the photograph in Plate I, fig. C, the surrounding branches having been broken off to expose the part. A tabula arises as a thin ring of smooth calcite about 0.1 mm. or less in thickness, projecting directly inwards from the side walls of the calix. Further growth enlarges the flat projection, and reduces the central pore leading to the basal part of the calix. Finally the pore is closed and a horizontal tabula is completed, leaving a closed cavity towards the axis of the branch, and forming a slightly convex floor to the calix (Plate I, fig. C). The process is then repeated, so that a series of tabulae is formed one outside another, cutting off chambers about 0.3 mm. in depth. Spines situated on the inner walls of the calix remain enclosed in these chambers. Where growth in diameter of a branch is most rapid the calix walls are fairly thick, and grow up so fast that few spines are found upon them. A series of tabulae is formed independently in adjacent calices, the rings first appearing at about 0.2 mm. below the surface, and on completion the tabulae lie about 0.3 mm. below the surface (Plate I, fig. C). The calices are here much shallowed than on the distal parts of the colony not showing the formation of tabulae (Plate I, fig. A).

SUMMARY.

1. The growth of individual branches of *Pocillopora bulbosa* during three months was studied. The colonies under observation were kept in the sea and were growing normally.

2. Linear growth of the branches took place mainly by the formation of new polyps at the tips by extra-calicial budding. Further down the branches growth took place by enlargement and separation of the corallites already present, together with the formation of tabulae; only occasionally were new polyps added here.

3. Details are given of the course of development of the polyps as seen externally in living material. Comparison may thus be made with the development of the young colony recorded by Stephenson (see Vol. III, No. 3 of these reports).

4. The mode of growth of the corallum is described, particularly the development of new calices and tabulae.

REFERENCES.

- DANA, J. D. 1846, 1849. U. S. Expl. Exped. VII, Zooph., pp. 740, 12, 61 pls.
- DUERDEN, J. E. 1902. West Indian Madreporarian Polyyps. Mem. Nat. Acad. Sci. Washington, VIII, pp. 399-648, pls. i-xxiv.
- 1903. Fissiparous Gemmation. Ann. Mag. Nat. Hist. ser. 7, XI, pp. 141-155, text-figs. 1-7.
- DUNCAN, P. M. 1885. A Revision of the Families and Genera of the Madreporaria. J. Linn. Soc. Zool., London, XVIII, pp. 1-204.
- EDWARDS, H. MILNE. 1860. Hist. Nat. Corall. III, Paris, pp. 1-560.
- GARDINER, J. S. 1897. On Some Collections of Corals of the Family Pocilloporidae from the S.W. Pacific Ocean. Proc. Zool. Soc., London, pp. 941-953, pls. lvi, lvii.
- HOFFMEISTER, J. E. 1925. Some Corals from American Samoa and the Fiji Islands. Pap. Dept. Mar. Biol. Carn. Instn., Washington, XXII, pp. 90, pls. 1-23, 1 map.
- KOCH, G. VON. 1896. Das Skelett der Steinkorallen. Festschr. C. Gegenbaur, II, pp. 250-276, pl. i, text-figs. 1-23.
- MATTHAI, G. 1926. Colony Formation in Astraeid Corals. Phil. Trans. Roy. Soc., London, B, CCXIV, pp. 313-367, pls. xxiv-xxviii, text-figs. 1-27.
- MAYOR, A. G. 1924. Growth Rate of Samoan Corals. Pap. Dept. Mar. Biol. Carn. Instn., Washington, XIX, pp. 51-72, pls. i-xxvi.
- ORTMANN, A. 1890. Die Morphologie des Skelettes der Steinkorallen in Beziehung zur Koloniebildung. Z. wiss. Zool., Leipzig, L, pp. 278-316, pl. xi.
- STEPHENSON, T. A. 1931. Development and the Formation of Colonies in Pocillopora and Porites. Part I. Great Barrier Reef Exp., Rep. III, No. 3, pp. 113-134, pls. i-vi, 16 text-figs.
- VAUGHAN, T. W. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. Washington, D.C., Smithsonian Inst., U.S. Nation. Mus. Bull. No. LIX, pp. 1-427, pls. i-xcvi.
- 1918. Some Shoal-Water Corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island. Pap. Dept. Mar. Biol. Carn. Instn., Washington, IX, pp. 49-234, pls. xx-xciii.

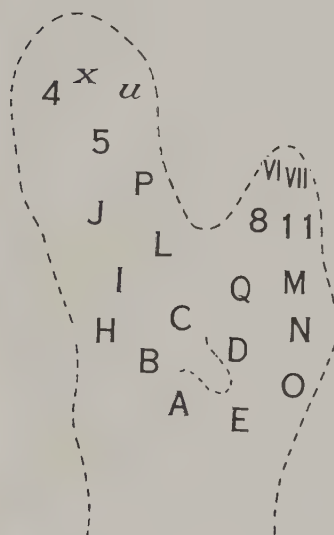
DESCRIPTION OF PLATE I.

FIG. *A* shows a photograph of the corallum on 27th June of the branch under observation and shown diagrammatically at various stages in Text-fig. 1. Fig. *B* gives a key to the numbering and lettering of the calices seen most clearly on the corallum and which can be compared with the side view of the living branch, Text-fig. 1, *D*, where the positions of the polyps are similarly marked. A key to the lettering and numbering is given with Text-fig. 1. Fig. *C* shows a photograph of the corallum at an angle between several branches, most of which have been broken off to expose the part more fully. This area shows tabulae being rapidly formed, and many are seen in various stages of development. For further description reference may be made to the text. *t*₁, tabula developing as a projecting shelf from the corallite wall. *t*₂, tabula nearly completed, the shelf being wider and the central space smaller. *t*₃, fully formed tabula, developed from a stage such as *t*₂ by obliteration of the central space. *t*₄, corallite split vertically, showing three successive tabulae.



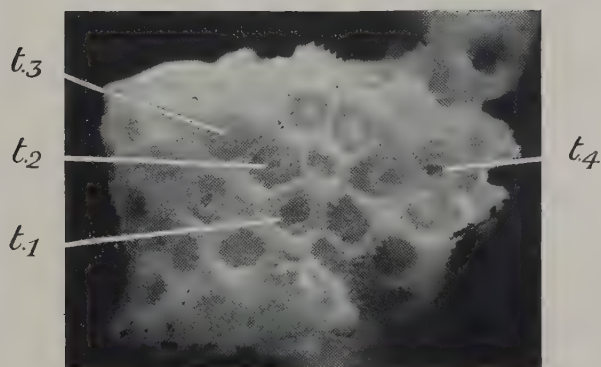
A

JUN 27



1
cm

B



C

GROWTH AND ASEXUAL REPRODUCTION IN CORALS

BY

T. A. STEPHENSON, D.Sc.,

Professor of Zoology in the University of Cape Town ;

AND

ANNE STEPHENSON

WITH FOURTEEN TEXT-FIGURES, TEN PLATES, AND NINE TABLES

CONTENTS.

	PAGE
PREFACE	167
MATERIAL AND METHODS	169
THE RESULTS OF THE PRINCIPAL EXPERIMENT	174
THE RESULTS OF SUBSIDIARY EXPERIMENTS	183
BUDDING IN ASTRAEID CORALS	190
THE RELATION BETWEEN FORM AND ENVIRONMENT IN CORALS	200
SUMMARY AND CONCLUSIONS	207
TABLES OF MEASUREMENTS	209
REFERENCES	216
SYSTEMATIC INDEX	217

PREFACE.

THE field work which formed the foundation for the results described in this paper was carried out by T. A. Stephenson, with the assistance, in the early stages, of F. W. Moorhouse, and later on of the natives Harry, Paul and Stephen, with incidental help from other sources. The photography was also done by T. A. Stephenson, with assistance in the development of films, at the end of the experiments, from M. A. Spender. Since our return from Australia the whole of the measurements have been made by Anne Stephenson, who has also enlarged a great many of the photographs and taken a large share in the preparation of both text and figures. We wish to thank everyone who helped us in the execution of a laborious piece of work, and especially F. W. Moorhouse, whose assistance at the beginning was invaluable ; and E. A. Fraser, whose notes and collections made on the Outer Barrier considerably extended the scope of our study of forms of growth in corals.

We are indebted to F. Pittock for photographs taken from collected material; and to S. M. Manton for the loan of three negatives, and for the specimens illustrated in Plate X, figs. 1 and 2. Prof. Matthai has very kindly identified many specimens for us, and the names here used are based on his determinations in most cases. A few species have been identified by T. A. Stephenson. The mollusca mentioned on p. 215 were identified by Mr. J. R. le B. Tomlin.

The question of growth-rate among corals has already received a considerable amount of attention, and experiments of some magnitude have been carried out by Vaughan (1916), Mayor (1924), and Edmondson (1929) in particular. Vaughan deals with Atlantic reefs, Mayor with Samoa and Fiji, and Edmondson with Hawaii. A series of observations from the Australian Barrier Reef therefore supplements these very suitably. With the addition of these new observations, we have now enough information to give us a fairly good idea of the way in which coral behaves in various parts of the world; but it will be only too evident to anyone who reads these pages that even now the gaps in our knowledge are numerous and sometimes wide. All the work mentioned when put together does not deal with a really large number of coral colonies. This is bound to be the case, from the very nature of the problem; experiments on a definitely large scale, often involving much transportation of heavy corals, could only be performed by teams of workers such as have not yet been available. Those which have so far been completed, however, serve to suggest lines of work which we hope will yet be followed up with profit.

We do not propose to give a history of what is known about coral growth. This has already been done, and the principal facts are reviewed in the papers mentioned in the last paragraph.

The main object of our experiments was to ascertain the normal rate of growth of a selection of different kinds of coral, belonging to the several growth-forms (massive, branched, etc.), which commonly occur upon reefs. We record here also the outcome of some subsidiary experiments, the results of which proved to be very interesting, although their scale was, by force of circumstances, much smaller than that of the principal experiment.

This series of experiments formed part of a programme of ecological work which was directed towards discovering the nature and distribution of the population of the Low Isles Reef, in relation to the several habitats available there, and its relation to the physical and chemical conditions prevailing in these habitats. A general account of the reef and its organisms has already been published (No. 2 in this volume); the present paper forms a second contribution to the subject, and reports dealing with other aspects will follow.

We suggest to future investigators that the following lines of work would repay further study. Along some of them a considerable amount of work has already been done; in other cases the field is almost untouched. The results recorded in the present paper will give some indication of the way in which such investigations might be expected to develop.

(1) An ecological comparison of coral habitats: The amount of growth which a coral achieves during a known period of time (if a sufficiently long period be allowed) may be taken as giving some index to its condition. It should therefore also give some indication as to the suitability of the habitat in which the coral is living, as a *milieu* for that particular coral species, provided always that due allowance be made for the operation of certain factors which affect its growth (see p. 174). In other words, the relative favourability of habitats may be compared by using corals judiciously as indicators. It is also

possible to compare the productivity of different parts of a reef (on the lines of Gislen's work on the epibioses of the Gullmarfjord), if the weights of skeleton deposited, and of coral tissue produced, are ascertained during the course of an experiment.

(2) A comparison of the normal growth-rate of a coral with the rate of regeneration in the same species, under various circumstances.

(3) A study of the changes in symmetry which take place in a colony as it develops. The normal course of the development of its characteristic shape should be ascertained, from the time of settling of the planula onwards, under circumstances which permit the coral to grow freely on all sides. This should be compared with the behaviour of corals which have at first been prevented by their surroundings from developing a normal symmetry, and which are subsequently transplanted to an environment where free extension in all directions is possible. Other comparisons in this sense will readily suggest themselves.

(4) A study of the growth-curves of coral colonies and species from the time of settling of the planula to the adult condition; with reference not only to the rate of development of the colony as a whole, but also to the behaviour of the ratio between the rate of deposition of skeletal material and the rate of increase in weight of the soft parts.

(5) Further investigation of the processes of asexual reproduction in corals, ascertained by direct observation on the living polyps.

(6) Further study of the problem of species among corals, both in the field and by means of experiment.

MATERIAL AND METHODS.

MATERIAL.—This report deals with the activities of 246 corals, all of which, with three exceptions, were collected at Low Isles. The exceptions came from Batt Reef. The Low Isles material was all collected either in the anchorage or in the Western moat.*

THE MEASUREMENT OF CORALS.—The difficulties involved in making accurate measurements of corals are realized only when an attempt is made to do it. Many corals are very irregular in shape, and in the case of branched forms this makes the measurement of a circumference, for instance, unsatisfactory. The measurement of diameters with a tape is also unsatisfactory. Diameters may be measured with calipers, but here the difficulty arises that it is necessary to mark in some way the diameter which one has measured. This may be done in the case of massive corals by driving small nails into them; but this is not, in practice, easily performed in a satisfactory manner, and has the disadvantage that it may induce abnormality at the very point where normality is most desired. In the case of branched corals, one may mark the branches at the ends of the diameter with wire. In such a case it is quite possible that the marked branch will be injured during the experiment; and in many branched forms it is actually impossible to get one's fingers between the branches, because they are too close together. Further, if the coral is to be marked *in situ* the measuring will frequently be complicated by the awkward shapes of surrounding rocks and corals, and, if the coral is in shallow water, the surface ripples which occur on most days in the year will render it impossible to see clearly what one's fingers are doing beneath the surface.

* These localities may be identified by reference to the key chart of Low Isles given in Report No. 2 in this volume, Text-fig. 2. Batt Reef lies some 7 miles to eastward of Low Isles.

We proved the truth of these objections by trial ; and as a result, evolved a method whereby the coral to be measured would be twice photographed, once at the beginning and once at the end of the experiment, and the measurement could be made on the negatives. The method is somewhat elaborate, but gave excellent results. We describe it in the following paragraphs in the hope of helping future workers ; because we should have been most grateful, when we started our experiment, if we had possessed more details of the methods of our predecessors.*

THE EXPERIMENTS.—Four experiments were carried out, as follows :

Experiment I.—In this case 169 corals were used. They were attached by means of cement to 100 blocks of concrete, which were planted out on the reef in suitable places after the corals had been photographed. In this experiment all the corals whose measurements are recorded, with two exceptions, were planted out in pools situated within 100 yards of the localities from which they were collected.

Experiment II.—Here 11 colonies were used, each colony being divided into halves. The halves were mounted on 10 concrete blocks, which were planted out on the reef as before ; but in this case one half was placed in its natural environment, the other in an environment alien to it.

Experiment III.—In this case 30 colonies were marked *in situ*, by a diver working below the level of low water.

Experiment IV.—Clean materials of various kinds (p. 188) were fixed at several points on the reef, in the hope that coral planulæ would settle upon them. Thirty-six young colonies were obtained in this way.

CONSTRUCTION OF BLOCKS.—The concrete blocks used in Experiments I and II were made from sand and cement (3-5 parts of sand to 1 of cement) mixed with sea-water. The mixture was poured into a series of moulds formed by a frame consisting of eight detachable lengths of wood, fitting into one another in such a way as to bound nine rectangular cavities. The bottoms of the moulds were formed by a sheet of galvanized iron on which the frame rested. The size of the blocks so produced was about 11 in. by 10 in. by 2 in. On each block, while the cement was still soft, a number was impressed ; and two holes were made through it by the insertion of glass tubes wrapped in well-greased paper. These tubes were removed after the cement had set, and through the holes thus left large iron spikes were driven when the block was subsequently attached to the reef. The blocks were left in the moulds overnight, and were watered to prevent too rapid drying ; the next morning they were removed and trimmed, placed in the sea, and left there to "cure" for two or three weeks.

ATTACHMENT OF CORAL.—The corals collected for attachment to the blocks were all healthy specimens, and examples of reasonably symmetrical form were chosen where possible. Colonies of various sizes were used, but there was an upward limit imposed by the difficulty of transporting any colony exceeding a certain weight. The corals were subjected to as little exposure as possible ; they were brought up from the reef in buckets of water, and attached to the blocks, in a shady place, with a mixture of pure cement and sea-water of about the consistency of plasticene. The cement was allowed to set for about 10 to 15 minutes, after which coral and block were returned to the sea. By the next

* Our method gave information only as to increase in diameter and change in form of the coral as seen from above. We should have liked to record increase in height and weight also, but had neither the time nor the apparatus required for this.

morning the cement had set quite firmly, and the coral, if still healthy, could then be photographed and afterwards planted out in a suitable place on the reef. When collecting the corals prior to their attachment to the blocks, specimens were obtained, wherever possible, which could be removed from the reef with a piece of the rock on which they had been growing still attached to their bases. This prevented any direct contact between the cement and the living tissues of the coral.

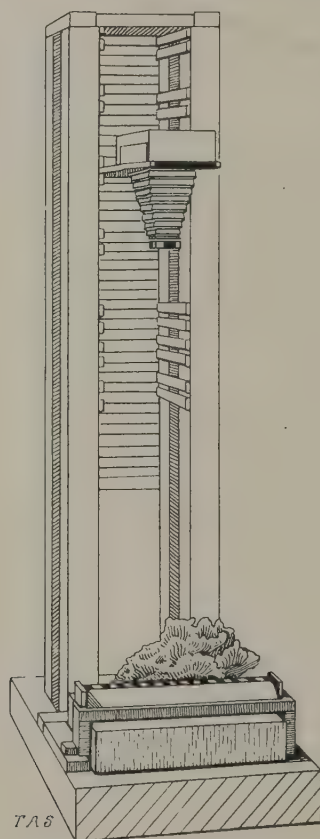
CONSTRUCTION OF PENS.—The number of people who had access to the reef, at low water, made it impossible to plant out experimental corals without protecting them in some way. We therefore decided to make two pens or enclosures, each containing a large pool surrounded by growing coral, and to plant out the blocks in these pools. The pools were therefore fenced in, the fences consisting of mangrove stakes driven into the reef with a sledge-hammer (a hole had to be made first with a six-foot crowbar), and laced together with stout wire. Since the floors of the pools were sandy, it was also necessary to make some provision against a silting-up of the experimental corals. This was accomplished firstly by arranging large boulders round the edge of the pool, and secondly by paving such parts of its floor as were not covered by cement blocks with flat slabs of beach-sandstone. All these paving materials had to be held in position by additional stakes and wiring; and the cement blocks themselves by means of 10-in. iron spikes. Even then the movement of sediment in one of the pools threatened to bury the blocks, and this was overcome by making a second series of blocks and mounting the first on top of them.

One of the pens was situated in the Western moat—a place in which the water was only just deep enough to cover the corals completely, during the period of low water. The physical and chemical conditions prevailing in this moat are described briefly in the general ecological report in this volume (No. 2, pp. 45–46), and will be dealt with in more detail by A. P. Orr in another report. We need, therefore, only say here that the conditions are those of a shallow tidal pool which may become very warm during low water, and which forms an environment unfavourable for the growth of many corals, although suited to that of a few species. The second pen was situated in the anchorage, in a place which was open to the sea at all states of the tide, and which became shallow enough to be visited on foot during low spring tides, but was at other times accessible only to a diver. The conditions were thoroughly favourable for a varied growth of coral, and the extremes liable to occur in the moat were largely eliminated. This environment also has been described in the ecological report (pp. 61–64), and will receive further attention from Orr.* The two pools, therefore, formed a contrast to one another, one representing a much more generally favourable environment than the other.

PHOTOGRAPHY.—It was necessary to construct some apparatus by means of which we could ensure that the two photographs of each coral, taken at the beginning and end of each experiment, should be taken from exactly the same angle. For this purpose the structure illustrated in Text-fig. 1 was made to our design by F. W. Moorhouse. It consisted of four strong wooden uprights, rigidly attached to one another, at the foot of which lay a horizontal platform upon which the cement block could be placed, the platform being firmly fastened to the uprights. Two wooden guides, raised above the platform, ensured that the block should occupy exactly the same position on it both before and after the experiment. That the camera should hold exactly the same relation to the block

* The temperature of the water in the anchorage was also ascertained twice daily, throughout the year, by F. W. Moorhouse. These observations will be published in another report.

on both occasions was also arranged by placing it, facing downwards, between the arms of a specially constructed wooden shelf which slid into a groove between the four upright pillars. Several such grooves were made, and were numbered, so that if need be the camera could be used at different distances in the case of different corals. A scale was introduced into the photographic field in the following way: A small wooden bridge was constructed, which could be placed astride the cement block, and could be replaced in a known position by means of guides, as in the case of the block itself. On the upper side of the bridge were fixed (1) a glass ruler on which had been painted approximate square



TEXT-FIG. 1.—Diagram of the apparatus used for photographing corals. This apparatus is described on pp. 171-2. Some of the details have been simplified or omitted in the diagram, in order to make clear the general arrangement of parts.

centimetres, and (2) an accurate slide-rule with its edge facing the camera. The photographs were taken with the smallest available aperture (F36), in order to ensure an adequate depth of focus, the camera being actually focused on the ruler. The results were satisfactory; the finest divisions of the slide-rule were sharply recorded on the negatives, and excellent definition was obtained in the outlines of the coral.

PROGRESS OF THE CORALS DURING THE EXPERIMENT.—Experiments I and II were started in September, 1928, and ended in May, 1929. When the corals had once been established in the pens they required no attention beyond periodic inspections, during which any dead colonies were removed, and details were noted of any sick or injured specimens. Unduly troublesome pieces of debris or accumulations of sediment, or algae, which had caught in the branches, were removed at such times. For the most part the condition of the corals remained excellent in both pens throughout the experiment. The number which died or were too much broken for re-measurement was 36 in a total of 180—20% of the whole. A number of the casualties were due to the blundering activities of large fish which from time to time visit such pools.

On 28th February, 1929, after heavy rains, flood-water from the Daintree River (the mouth of which lies a little to the north of the reef on the adjacent mainland) swept a large amount of mud and debris into the sea. The effect was so marked that the sea all round the reef became peaty-brown in colour, and partially opaque. When the pen in the moat was visited on the next day the corals were not visible at all in 3 ft. of water. On 4th March the water had cleared and the corals were examined. A large amount of flocculent sediment had collected, but apparently with little ill-effect. A number of deaths had occurred, but the dead specimens were all more or less brown and covered with algæ, which means (see p. 205) that they probably died *before the flood*. The cause of their death, we believe, was a spell of unusually hot weather coinciding with spring tides, which had preceded the flood, and during which a number of coral deaths on the reef outside the pens had been noted.

On 22nd April, 1929, a large proportion of the corals in the anchorage pen were found to be covered with an extensive growth of beard-like Cyanophyceæ (of a type similar to *Lyngbya majuscula* or *Hormothamnium solutum*), some specimens being almost hidden by it. This growth had come into being during the preceding three or four weeks, and seemed to be generally prevalent in the anchorage.

As we had no knowledge as to what effect these smothering algae would have on the corals, the experiment was ended on the next day.

PROCEDURE IN EXPERIMENTS III AND IV.—The method above described applies to Experiments I and II, and that used for no. IV is described on p. 188. In Experiment III, where the corals were marked *in situ*, a different method was adopted. A. In a number of colonies the ends of individual branches were broken off, each broken branch being marked with a ring of silver wire, and each colony with a silver label bearing a stamped number. The object of this procedure was to obtain data respecting the regeneration of the broken branches. In the cases of other colonies, where the branches were too close together to permit of convenient individual marking, a loop of silver wire was tied round the bases of a group of branches, and all the branches within the loop were broken. B. There are certain species of *Acropora* which form shelf-like or cyathiform colonies, in which the branches on the upper surface are all fairly even in length. It occurred to us that if we killed some of the branches in such corals, by placing a cap of plasticene over their tips, we should be able to ascertain approximately the amount of growth of the undamaged branches, by noting the difference in level between the living and dead branches, after a suitable period had elapsed. This method would probably give good results if carried on long enough; but in our own case we tried it too near the end of the time available, and the amount of growth which occurred was not enough to give a satisfactory result.

THE RESULTS OF THE PRINCIPAL EXPERIMENT.*

(EXPERIMENT I.)

(The Growth of Corals Mounted on Cement Blocks, in their Natural Environment.)

A. FACTORS WHICH AFFECT CORAL GROWTH.

In considering the results of the experiments, a number of factors which may be expected to exert some influence on coral growth must be considered. The factors in question are the following :

(1) INCONSTANCY OF GROWTH RATE.—It was noted by Wood-Jones (1910, p. 69) that corals do not necessarily grow at an even rate, but may increase by fits and starts. He showed that one coral might grow rapidly for a time, and make no further progress in the succeeding period ; whilst a neighbouring colony might be quiescent during the period within which the first had been active, and grow again while the first was in its passive phase. Such periods may alternate with one another irregularly, and have no connection with any known cause. These observations were confirmed by Mayor (1924, p. 52) and Edmondson (1929, p. 20). The experiments described in this paper do not add further evidence on this count directly, since each coral was measured twice only ; but an analysis of the figures shows that the exact length of the experiment bears no direct relation to the amount of growth achieved, and that its exact duration affects the amount of growth recorded less than any of the other factors involved. This result is doubtless to be ascribed, in part, to the effects of an erratic rate of growth, and may be regarded as an indirect confirmation of the conclusions of previous workers.

This irregularity of increase renders the interpretation of results distinctly complicated ; one must constantly be on the watch for effects which may be due to it, and it is not always possible to distinguish such results from those which are in reality due to other causes. In the following sections an attempt is made to evaluate some of the other factors which undoubtedly contribute to the determination of the amount of the growth which a coral will make, but it must be remembered that the intermittent nature of the growth will complicate these discussions in greater or lesser degrees. It seems to be clear, however, that apart altogether from the influence of the spasmodic rate, there are other recognizable effects due to environment and to the age of the coral. Although the figures bearing on these latter factors are complicated by the former, the results of the several influences can be disentangled fairly easily. In the case of individual variation the separation of effects is more difficult, but even here both the individual variation and the uneven growth-rate appear to contribute to the actual result.

In the present experiments the period of growth allowed to the corals was not quite the same for all of them. Sometimes it was the same for any two colonies, or differed only by a few days or a week ; in other cases there was a difference of several weeks. In the case of those corals which were kept in the anchorage the maximum variation in period of experiment between any two of them was 25 days ; in the moat the maximum was 30 days. Only when moat and anchorage corals are compared with one another (and this comparison is rarely made) does any question of a discrepancy of more than a month arise.

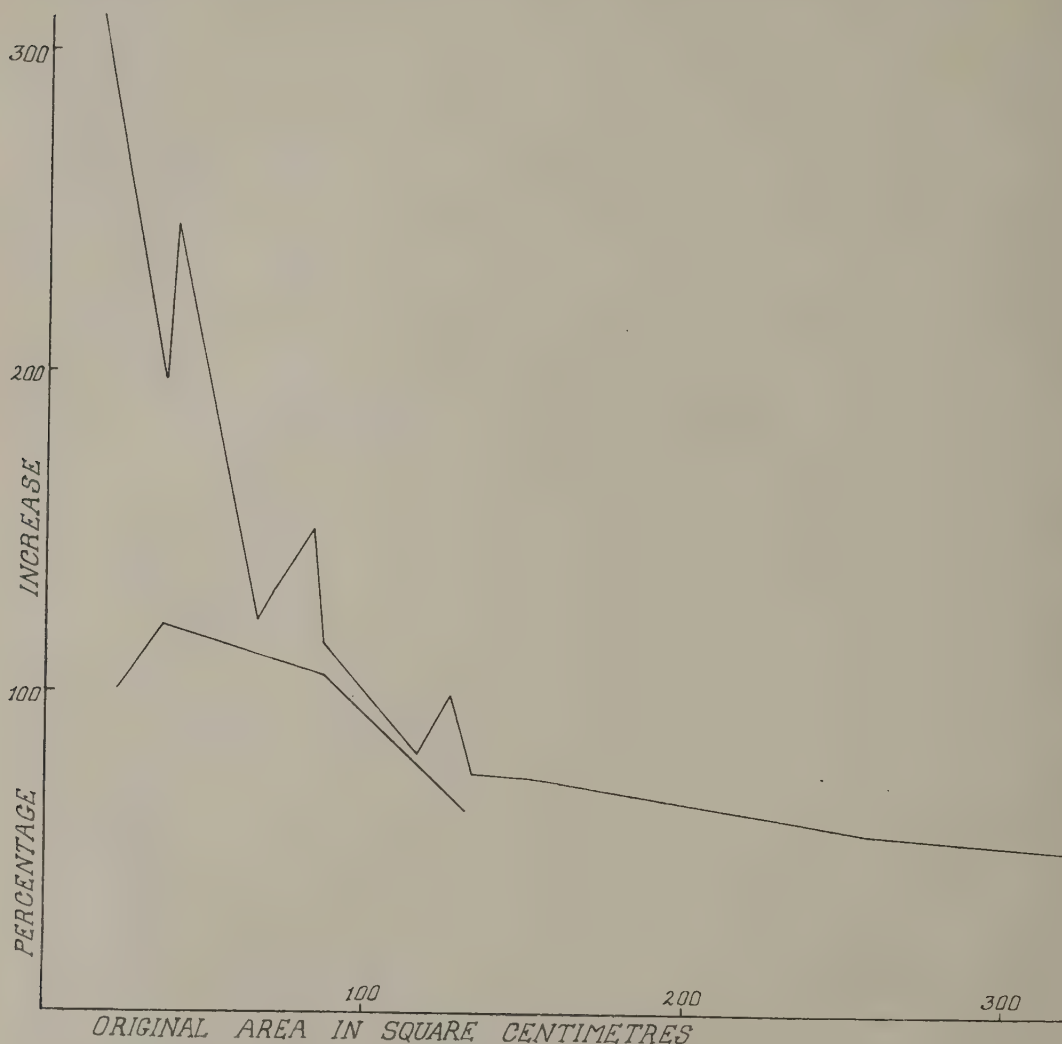
* The measurements made in connection with both the principal and subsidiary experiments are recorded in full in the tables at the end of the paper.

We have already seen that a difference in experimental period, of the order here involved, happens to have no significance for the interpretation of the results, beyond what has already been ascribed to it. At the same time it should be explained that the only reason why the period was not the same for all the corals was that in the case of experiments as laborious as those described, it is a physical impossibility to begin the experiment on a given day or even in a given week, unless a large number of persons are able to engage in it at once—a condition which could not be met on the present expedition. This will be readily appreciable to anyone who considers carefully the amount of manual work involved in the several stages of the method adopted; besides which the time available for such work on any one day or in any one month is limited by the tides (the anchorage pen being inaccessible except by diving, even at low water, on many days), and by sunshine (the corals can only be taken out of the water in the cooler part of the day). The one factor which is important is that the minimum experimental period should not be too short; and this condition was satisfied.

(2) ENVIRONMENT.—That a coral may grow very much more in a favourable environment than in a less favourable one is demonstrated clearly by cases such as the one illustrated in Plate VII, figs. 5–7. The two pens in which the experimental corals lived were subject to two different combinations of environmental conditions, one series more favourable to coral growth in general than the other. The growth of corals in the anchorage should therefore be considered separately from the growth of corals in the moat. On the other hand, this effect of environment should not be given too much weight. Its incidence is very different for different species of coral, and it applies chiefly to the more delicate forms which *normally live in the anchorage*, and which die or flourish less well in the moat. In the case of species which normally live in the moat, or which will live there fairly successfully, there appears to be little or no difference in the effects of the two environments upon growth.

(3) SIZE OF COLONY.—If a small colony and a large colony of the same species are taken, and are allowed to grow in the same environment and for the same length of time, one of them may grow proportionately much more than the other. In such a case the chances are that the small colony will grow more in proportion than the large one; but this is not necessarily the case, and the opposite may occur, particularly if the difference in size between the two colonies is not great. An example of the former occurrence is given in Plate I, figs. 3–6, and Plate II, figs. 1 and 2, in colonies of *Acropora squamosa*. The colonies illustrated in Plate I, figs. 5 and 6, and Plate II, figs. 1 and 2, were both kept in the anchorage, and the period of the experiment was 29 weeks and 2 days for both. The growth in the larger colony was 34% on each of two diameters, that in the smaller colony 106% and 105% on two diameters. The still smaller colony of Plate I, figs. 3 and 4, grew in the less favourable environment of the moat, and might therefore have been expected to grow less actively; and it was allowed to grow for 5 weeks longer than the others. With the last factor in its favour and the first against it, it achieved the enormous increase of 150% and 185% on two diameters; this difference is of such magnitude as to discount the effects of time and place, and is clearly correlated with the vigorous individual growth-power of the colony, which, though very small, grew far more in proportion than its larger counterparts in the anchorage. An example of the opposite state of affairs may be obtained from other colonies of this same species of *Acropora*. Colony No. 40a and Colony No. 57 were both healthy specimens of *A. squamosa*. Both were kept in the anchorage,

and the period of experiment was the same for both but for a difference of 4 days, which can have no significance. No. 57 was much larger than No. 40a, but it grew distinctly more strongly, its increase being 34% on each of two diametres, as against 29% and 26% in No. 40a.



TEXT-FIG. 2.—Graphs summarizing the data obtained by measuring the increase in area of 17 colonies of *Pocillopora bulbosa*. By "area" is meant the area covered by the coral; the comparison was effected by measuring the area of the projected image of the coral, before and after the experiment, on an enlarged photograph, with a planimeter. It will be noted that the increase for the smaller colonies is progressively greater than for the larger ones, and that all the specimens with an original area of less than 100 square centimetres have increased this area by 100% or more, up to the large increase of 310% in the youngest colony. The upper graph represents growth in normal colonies; the lower graph refers to half-colonies which were regenerating. For further comment, see p. 177.

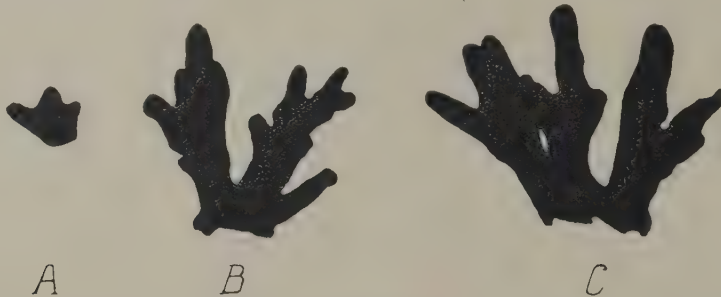
Since variations of the nature just described are to be found in the amount of growth achieved in the same species, irrespective of environment, time, and size of colony, it is clear that if one attempts to construct a growth-curve for any species of coral, the individual points plotted will necessarily often lie wide of the curve itself. In the experiments here described, the number of colonies used for any single species was usually too small to enable us to construct a curve for it (nor was it our object to do this), but in one case, that of *Pocillopora bulbosa*, the data appear to lend themselves to this treatment fairly well. We wish to make it clear that, since the data presented for *Pocillopora* are few, we do not desire to base a final conclusion upon them; but they are so interesting and suggestive that we should like to put them on record in the hope that future workers will carry out further work on the same lines with much larger numbers. It may be pointed out, however, that even if a larger experiment involving hundreds of colonies were carried out, this would not eliminate the peaks and depressions which occur in the present graphs. These are due to normal individual variation and would always persist; but a large experiment might bring a majority of the points close to a definite curve. In the presentation of the lower graph in Text-fig. 2, specimens of the coral grown in moat and anchorage are treated together (the upper graph is based entirely upon moat-grown colonies); this is legitimate for the species in question, because it is one which both in nature and in the experiments grew well in both environments. If any conclusion may be drawn from Text-fig. 2, it is that in *Pocillopora bulbosa* the amount of growth falls off at a fairly definite but not constant rate as the colony grows larger; and that in specimens which have been divided and are regenerating the amount of growth is, for a time, considerably less than in normal specimens. It has been shown by Vaughan and Mayor also that as certain corals grow older their rate of growth declines.

(4) INDIVIDUAL VARIATION.—This factor is probably a potent one. Two corals belonging to the same species, growing in the same environment, for exactly the same length of time, can and do show striking differences in the amount of their growth, even though both are perfectly healthy and normal. We have already seen that such variation is sometimes correlated with differences in size, but also that it sometimes occurs irrespective of these. This variation means that the results of any experiment are bound to give very irregular figures, so that in summarizing the results in general terms it is preferable to use averages rather than to rely too much upon individual figures. As further examples of such variation we may take the following. In two colonies of *Acropora quelchi*, of approximately the same size and shape (10.85×10.13 cm. in the one case, and 11.20×9.96 cm. in the other), both growing in the anchorage, the increase in the first case was 57% and 78% on the two diameters, in the second 44% and 34%; this is a little further emphasized by the fact that the colony which grew the lesser amount had three weeks longer in which to do it. Again, in two colonies of massive *Porites*, measuring respectively 8.26×8.10 and 8.69×7.77 cm., both growing in the moat, the increase in the former case was 22% and 24%, in the latter 8% and 6%. In this instance there was a difference of two weeks in the experimental period, in favour of the colony which grew the most, but this can have had no more than a small effect on the result. The effects of individual variation in vigour of growth are not easily distinguished from those due to intermittent growth-rate; but in cases such as these, where the effect is considerable, it is probable that both factors are involved.

(5) THE FORM AND INTERNAL STRUCTURE OF A COLONY are obviously factors which

affect its rate of growth. A branched species may be expected to grow more rapidly than a massive one, and a species with slender branches more quickly than one with stout branches. Further, a coral of loose porous texture should grow more rapidly than one with a firm and dense skeleton. These expectations are, in general, confirmed by the results. They do not work out quite mechanically, but that again is to be expected.

CONCLUSIONS.—From the foregoing paragraphs, we may conclude that the most powerful of the factors which determine what the growth of a coral will be within a given period are the relation between its spells of active growth and spells of quiescence; its individual vigour or growth power; its shape, size and environment. The size factor will not be effective in every case; but it is evident that, apart from the factors of individual variation and spasmodic rate of increase, there is a distinct tendency for young corals to grow more rapidly than older ones. The next effective factor is that of environment; this will clearly determine where corals can establish themselves at all; but apart from this, it will affect some species much more than others. If a reef presents more



TEXT-FIG. 3.—Silhouettes of young colonies of *Montipora ramosa*, illustrating the growth that they made in 8 months. A and B represent the same colony at the beginning and end of the period; C represents a colony which started from a beginning which was probably even smaller than fig. A. All figures are to the same scale, about three-quarters natural size.

favourable and less favourable environments, certain species will be able to grow well in both, whereas others, if they can survive at all in the less favourable habitat, will grow but little there and will not reach a large size. There are intermediates between these two extremes. Lastly, the length of the given period will operate in this manner; if it is very short, the effect of the intermittent growth-rate may mask all others; if it is as much as several years, the effects of age and of average growth will become apparent; but if there is any question of a difference such as that between 6 and 9 months, this may have no effect, since it is quite possible for one coral to grow more in 6 months than another of the same species does in 9, for the reasons already stated. In connection with periods of several years, it should be remembered that corals reach limiting sizes at different ages, according to species, and that some of them probably normally live for a few years only.

In interpreting the figures presented in this paper all the factors just mentioned must be taken into account.

B. FURTHER CONSIDERATION OF THE RESULTS.

(1) THE COMPARATIVE GROWTH-RATES OF THE CORALS USED IN THE EXPERIMENT.—We have seen that it is advisable when considering the general results of a certain class

of experiment to use averages rather than individual figures. The averages presented are based upon perfectly healthy and normal colonies only, subnormal cases or specimens which died before the end of the experiment being omitted.

The average rates for a number of the colonies measured are summarized in the following table. It will be observed that the highest average increase recorded is that for *Montipora ramosa*, one of the commonest of the moat-dwelling species. If this average were based on a larger number of colonies (the casualties in this species were high, so reducing the number available for measurement), it would no doubt approach the average for *Acropora* more closely; but the astonishing rate of increase in the young colony of *M. ramosa* might even then raise the figure. This remarkable growth is illustrated in Text-fig. 3, which represents the history of two small colonies during a period of 31–32 weeks. In Figs. A and B we have silhouettes of a small colony at the beginning and end of the period, the increases on 3 diameters being 197, 206 and 237%. Fig. C is the silhouette of another young colony which sprang up from a beginning so small that it is not visible at all in the first photograph, being probably overhung by a large *Favia*. The original size of this colony is unknown, but at the end of the experiment it was larger than B, and apparently came from an even smaller beginning, so that the percentages here would be higher still.

Genus.	Average percentage increase in diameter. Based on the mean increase on two diameters.	Range of percentage increase in each genus.	Number of colonies upon which average is based.
<i>Montipora (ramosa)</i>	95	42–227	3
<i>Acropora</i>	57	13–185	35
<i>Pocillopora</i>	43	14–80	13
<i>Psammocora</i>	33	14–57	9
<i>Porites</i>	17	6–37	5
<i>Favia</i> and <i>Coeloria</i> *	10	3–22	17
<i>Lobophyllia</i>	10	$\frac{1}{2}$ –23	11
<i>Symphylia</i>	10	1–29	6

* The species of *Favia* (with its subgenera) and *Coeloria* are treated together here, because the only species of *Coeloria* involved was *C. daedalea*, which, in the colonies used, was very little meandrine. The species grouped together all belong to one form as far as growth is concerned.

After *M. ramosa* comes *Acropora*, with an average of 57%; then the other branched forms, *Pocillopora* and *Psammocora*, with averages of 43% and 33%. The massive species of *Porites* form a link between the high rates (over 30%) of the branched corals and the low rates (10%) of the Astraeid genera *Favia*, *Coeloria*, *Lobophyllia* and *Symphylia*. The position of *Porites* in this scale is interesting, in view of the fact that it forms a considerable percentage of the reef-substance in some of the reefs of the Great Barrier region. Its relatively rapid increase is probably connected with the fact that it is a perforate coral, whereas the Astraeids are imperforate.

(2) FURTHER DETAILS FOR CERTAIN GENERA.—*Acropora*.—The variety of growth-form in this genus is very great, as an inspection of the plates illustrating this paper will

make clear. Some of the extremes of form, however, are not found among the species used in the experiments—*e. g.* the largest types of stagshorn coral, the massive species such as *A. palifera*, and certain encrusting forms. Seven species (apart from a few small undetermined colonies) were used in Experiment I, and all of them proved to be rapid growers; but the actual rate naturally varied to some extent from one species to another, as well as from one colony to another within the same species.

We cannot give much information with regard to the relative *average* growth-rates of the seven species (although measurements of 43 colonies are given in our tables), because it was not possible to obtain, for the experiment, a reasonable number of colonies of every one of them; moreover, there were more colonies broken (by fish, etc.) during the experiment in some species than in others. Thus we were able to obtain measurements in the end from thirteen colonies of *Acropora squamosa*, and from fifteen colonies (including three varieties) of *A. quelchi*; but in the other cases the number was fewer, and in two species only a single colony survived. The average figures for each species, based on such numbers, could not be reliable. The conclusions stated in the next paragraph, however, probably represent the truth fairly closely.

Of the seven species used, one, *Acropora gemmifera* (Plate III, figs. 3 and 4), has as a rule more massive thumb-like branches than the others: this species appears to grow more slowly than the remaining ones. Which of the species grows most rapidly we cannot be certain; but two of them certainly grow very quickly indeed. Our only specimen of *Acropora hyacinthus* (Plate II, figs. 5 and 6), a young one, showed an increase of 99 and 127% on two diameters. This does not parallel the increase of 150 and 185% exhibited by a young specimen of *Acropora squamosa*; but in the case of *A. squamosa* (Plate I, figs. 3-6; Plate II, figs. 1 and 2) eleven normal colonies were available for measurement, and the average increase for these was only 54%. On the other hand, an average for *A. hyacinthus* would probably be higher than this, because it has more slender branches than most of the species used, and can probably grow quickly even when older. Another species which undoubtedly grows very fast is the stagshorn *A. pulchra* (Plate I, figs. 1 and 2), with branches of moderate thickness; here an average for four colonies gives an increase of 66%, and the performance of three of the four colonies measured was much greater than this. The remaining species are of intermediate standing. *Acropora squamosa*, and *A. quelchi* (Plate II, figs. 3 and 4) in its several varieties, have branches of intermediate degrees of thickness; these showed intermediate average amounts of growth, and would probably occupy an intermediate position on any computation. *Acropora exilis* (Plate III, figs. 5 and 6) did not increase strikingly in total diameter, in spite of its slender branches; but this is a species with more lateral subdivision of its branches than the other species measured, so that a good deal of its growth would be diverted into the lateral branches, and would not affect the total diameter of the colony. The single colony of *Acropora formosa*, a slender stagshorn, grew less than might be expected.

Montipora. The rapidity of growth in the branching species *M. ramosa* has already been mentioned (p. 179). The type of increase which takes place in the foliose species is illustrated in Plate IV. The growth here is less rapid than in *M. ramosa*, but is nevertheless of considerable amount.

Seriatopora.—The single colony belonging to this genus increased 19 and 29% on two diameters. In this case the *upward* growth of the slender branches was probably greater than their lateral extension.

Astraeidae.—It has been seen already (p. 179) that the average amount of increase in *Favia* and *Coeloria*, *Lobophyllia* and *Symphyllia* is the same (10%). In addition to these, two colonies of *Galaxea musicalis* were measured. These gave an average increase of 10% also.

Fungida.—The results with specimens of *Fungia*, *Döderleinia* and *Herpetolitha* were distinctly curious. These forms do not lend themselves very well to attachment to a cement block, because the cement is bound to kill part of the flesh on the aboral side of the disc, and the attachment of a more or less flat coral to a flat block leaves it very much exposed. Notwithstanding this, the health of some of the specimens seemed to be excellent throughout the experiment. A specimen of *Fungia actiniformis* var. *crassitentaculata* was attached to a block in the anchorage pen. It was a large specimen, the skeleton measuring 17.5×18.5 cm. In this species the skeleton is as a rule invisible during life, being hidden under a mass of waving tentacles, the inner of which are some 6 in. in length. The expanded polyp is therefore much larger than the skeleton, and is a very conspicuous object. This coral suffered severely at first from contact with the cement; it changed from brown to nearly white; the tentacles became reduced, and the mouth gaped. The specimen appeared to be dying. Very shortly, however, it began to recover, and six weeks after it had been attached to the block it was thoroughly flourishing once more, with long brown tentacles and a closed mouth. It remained perfectly healthy until the end of the experiment, but did not increase in size by any measurable amount (the 0.4% increase quoted in the table on p. 212 is within the region of experimental error). Another specimen attached to a block in the anchorage, but belonging to a different species (*F. fungites*, one of the green and purple *Fungia*e whose tentacles expand only at night), suffered considerable retraction of its flesh at first, but also recovered completely in less than six weeks. This one also grew an inappreciable amount. Five specimens of another night-flowering variety which normally inhabits the moats were attached to blocks in the moat pen. None of these suffered any inconvenience from their attachment, but three of them died before the end of the experiment. The amounts of growth they exhibited, however, were very varied—from no appreciable increase (3% on one diameter and none on the other) in two cases to 10% and 13% on two diameters in another, the latter case being one in which the coral died 23 weeks after the beginning of the experiment. The specimens of *Döderleinia* and *Herpetolitha* were healthy throughout the experimental period, but increased by very small amounts (average increase 3%). Of the compound *Fungids*, *Psammocora* and *Pavona* were used. The results for *Psammocora* have already been noted (p. 179). Two portions of a large colony of *Pavona cactus* gave an average increase of 16%, and the development of one of these pieces is illustrated in Plate V, figs. 1–3.

Alcyonaria.—A few records of growth in the fleshy alcyonaria which form a considerable part of the population of the seaward slope of the reef are given in the table on p. 212. The three colonies measured give an average increase of 47%, and one of them is illustrated in Plate VI, figs. 5 and 6. One large colony of *Heliopora coerulea* was used. This colony probably died soon after the beginning of the experiment; but appeared to be in a state of suspended animation for a time, so that the exact time of its death could not be determined. In any case it grew only a very slight amount.

(4) A POSSIBLE DIFFERENTIAL GROWTH-RATE IN CORALS.—It will be shown farther on (p. 186) that when broken corals are regenerating, some of their branches may

regenerate much more rapidly than others. In some cases this inequality in regeneration appears to be quite irregular and directed towards no particular end; in other cases it appears that there is a fairly definite normal shape towards which the growth of the colony tends, and that if this normal shape is impaired by damage, branches will regenerate, or will grow out from neighbouring branches, to fill the gap, and will grow rapidly until the normal shape is restored. This is illustrated by the colony of *Pocillopora* described on p. 188, and represented in Text-fig. 4 and Plate VII, figs. 3 and 4.

It occurred to us that if so marked a difference in growth-rate may distinguish the individual branches of a regenerating coral, some less definite but still appreciable effect might be detected in the growth of a normal colony. An examination of the figures suggests that such an effect is demonstrable. In the following table some of the data obtained in Experiment 1 are summarized:

Genus.	Average percentage increase on greater diameter.	Average percentage increase on lesser diameter.	Number of colonies in which increase on greater diameter is greater than that on lesser diameter.	Number of colonies in which increase on greater diameter is equal to that on lesser diameter.	Number of colonies in which increase on greater diameter is less than that on lesser diameter.
<i>Montipora (ramosa)</i>	76	114	0	0	3
<i>Acropora</i>	52	62	14	1	20
<i>Pocillopora</i>	37	50	2	0	11
<i>Psammocora</i>	31	36	3	1	5
<i>Porites</i>	16	18	2	0	3
<i>Favia</i> and <i>Coeloria</i>	9	10	5	4	8
<i>Lobophyllia</i>	9	10	3	0	8
<i>Symphyllia</i>	8	11	1	0	5
Totals for the several genera			30	6	63

Total number of colonies to which the data refer, 99.

From the first two columns of the table the curious fact emerges that, in the 99 colonies to which these data refer, *the average percentage increase on the lesser of the two diameters measured exceeds the corresponding increase on the greater diameter in all the genera included in the table.* This suggests that if a coral is wider across one diameter than it is across another, it tends to grow more quickly where it is narrower; in other words it tends to grow in such a way as to cover a roughly circular area.* That this, if true, is a tendency and not an invariable rule, however, is shown equally clearly by the remaining columns in the table, from which it is evident that of the 99 colonies measured, 30 provided exceptions to the general tendency. Even then, a majority of 69 in 99 in favour of the existence of the tendency is fairly satisfactory, especially since some at least of the exceptions can probably be accounted for by special reasons operating in their particular cases.

A coral can naturally grow in such a way as to cover a circular area only if it has free space all round it so that it can extend in all directions. This condition is often absent in nature, since the coral may be prevented by rock, or by other corals, from extending

* We should say, from general observation on the reef, that such a tendency does exist. It does not, of course, apply in the case of corals of special shapes—e. g. *Herpetolitha*.

in given directions ; or may even be hemmed in all round. In the case of corals mounted on cement blocks, however, the colony usually has all the freedom required.

THE RESULTS OF SUBSIDIARY EXPERIMENTS.

Before describing these results we may point out that in Experiment 1 the number of coral colonies used (169) was large for a laborious experiment of this nature carried out by a few persons. In the case of the subsidiary experiments much smaller numbers had to suffice ; these experiments were side-lines-for which we were able to spare a little time only. This is the only reason why larger numbers were not employed. The results, nevertheless, proved to be interesting.

EXPERIMENT II.

(*Transplantation of Corals to Different Environments.*)

Eleven colonies formed the material for this experiment. Each colony was divided as evenly as possible into two portions. The halves were attached to cement blocks as in Experiment I, and were planted out in the same two pens which were used for that experiment. One half of each colony was planted in the pen representing its original environment as a control ; the other half was planted in the contrasting environment. In other words, if the colony was collected in the moat, half of it was maintained there and the other half was transferred to the anchorage ; and *vice versa*.

The results of the experiment are recorded in tabular form on p. 213. It may be noted that none of the colonies appeared to suffer any harm from being divided into halves. Any disturbance caused by the operation was too slight to affect their health, even though it may have affected their rate of growth during regeneration.

Pocillopora bulbosa.—This species normally lives and flourishes in the moats. One would therefore expect that the halves kept in the moat would flourish, and that those planted in the anchorage (a locality more favourable to coral growth, to all appearance, than the moat) would do likewise. The four halves used in the experiment bore this out ; all survived and grew excellently.*

Montipora ramosa.—This again is a species which normally inhabits and flourishes in the moats. One colony was divided, and both halves achieved good growth. Whether the fact that the half kept in the anchorage grew more than the one in the moat has any significance, it is impossible to say on the basis of a single example.

Montipora.—A foliose species (Plate IV, figs. 1 and 2).—This was a colony belonging to one of the more delicate foliose species which, so far as we know, never occurs in the moat, where only certain coarser foliose forms are occasionally found. It is a typical open-water species, and our general experience suggested that it would not survive moat conditions. The result of the division of a single colony bore this out ; the half planted in the moat died very soon after transplantation ; the anchorage half flourished and grew well.

Acropora exilis and *Acropora formosa*.—These, again, are species characteristic of

* The great discrepancy between the increase on the greater and lesser diameters recorded in the case of No. A4 is apparently due to the fact that this colony was flat on one side, and that rapid growth on the lesser diameter took place, thus restoring the colony to reasonable symmetry. The case of this colony is dealt with in detail on p. 188.

open water, not normally found in the moat, and to all appearance of delicate constitution. One colony of each was divided. In both cases the halves kept in the anchorage flourished and grew strongly; and the halves kept in the moat died. In the case of *Acropora exilis* death occurred within a few days of transplantation; in that of *Acropora formosa* the colony died more slowly, and a single twig survived some time longer than the rest, but ultimately succumbed.

Acropora quelchi, var. 1.—This is a somewhat mysterious variety. It is a form of neat and characteristic appearance, common in the western moat, where it forms small colonies or small brackets. The branches are often blue-tipped. It has the appearance of being a young or stunted form of some species whose normal habitat is the seaward slope of the reef, and appears likely to be a modified form of *A. quelchi*. In the case of the single colony divided, the half kept in the anchorage grew well; that kept in the moat survived but made no progress.

Acropora squamosa.—This is a species characteristic of the anchorage, and attains normal stature only in open water. It is not uncommon, however, in the moat, but only in the form of young colonies; occasional larger colonies are to be found there, but always of subnormal size. A single colony was divided. Both halves survived, but the one kept in the anchorage grew much more strongly than the other.

Acropora hebes.—This is the only species of *Acropora* which normally flourishes thoroughly well in the moat (speaking of Low Isles only). Other species occur there, but usually only as young or exceptional colonies. It would therefore be expected that *A. hebes* would flourish both in moat and anchorage. Two colonies were divided. Unfortunately the moat-half died in one case, and the anchorage-half was broken by a large fish in the other (though it grew satisfactorily until broken). The two surviving halves, however—one in the moat and the other in the anchorage—both flourished and grew strongly. The growth achieved by the half kept in the moat is illustrated in Plate VII, figs. 1 and 2.

Acropora, species 1 (undetermined).—This species normally occurs in the anchorage, and only as young or struggling colonies in the moat. A very young colony from the moat was taken, and was divided. The remarkable result is illustrated in Plate VII, figs. 5-7, and is described on the page facing the plate. The result is a striking example of the way in which the growth of an organism may provide an index to the relative suitability of the two environments to the needs of a given species. It is true that one could not make any generalization from a single example, but the case is not the less suggestive on that account. The following data are direct measurements of the lengths of 10 branches in each of the two halves of this coral at the end of the experiment, and provide a means of comparing the growth of the two halves.

Lengths of individual branches in the half kept in the anchorage, measuring from base to tip.		Lengths of individual branches in the half kept in the moat, measuring from base to tip.	
70.4 mm.	80.75 mm.	30.5 mm.	33.0 mm.
80.0 "	80.95 "	31.25 "	34.5 "
80.0 "	90.05 "	32.55 "	36.0 "
80.55 "	90.25 "	32.75 "	36.5 "
80.7 "	90.95 "	32.85 "	38.25 "

CONCLUSIONS.—In an experiment dealing with 22 half-colonies only it is obviously not possible to generalize from the result, since it is always possible to maintain that the results may be due to accidents. On the other hand, in a case where general experience gained in the field leads to certain definite expectations, and in which these expectations are exactly fulfilled in 21 out of 22 cases (the single exception certainly *was* accidental), we have at least some reason to suppose that we are on right lines, and that the results of a larger experiment would bear out those of the small one. We think, therefore, that the following conclusions are probably justified :

(1) The species used which are normally inhabitants of the moat grow well both there and in the anchorage.

(2) The species used which are normally inhabitants of the anchorage either die in the moat, grow less well there, or fail to attain normal size.

EXPERIMENT III.

(Regeneration of Branches in Colonies of Acropora.)

This experiment was concerned with the marking of 30 colonies (all of them but one belonging to the genus *Acropora*), and its object was to obtain information relating to the rate of regeneration in branches belonging to this genus. The corals in this instance were not removed from their own habitat at all, but were marked *in situ* by one of us (T. A. S.) from a diving helmet. They were all situated in two small areas near the mouth of the anchorage, both places lying well below the level of low water of the lowest spring tides, so that the depth of water over the corals would never be less than some 8 or 10 ft. It was found that marking could be carried on for an hour and a half at a time below water, but that longer periods than this were unsuitable.

The method by which the corals were marked has already been described in the section on material and methods (p. 173). Of the 30 colonies marked, only 11 were recovered at the end of the experiment. This is due partly to the fact that the ones which had been marked with plasticene (p. 173) had not developed far enough to give a result ; and partly to the fact that some of the colonies could not be re-discovered by the diver. This latter point will not surprise anyone who has worked below water, and who knows how short a distance before one it is possible to see, under submarine conditions. (It was not feasible under the circumstances to mark each colony with a buoy.)

When the material was recovered at the end of the experiment, sometimes the whole colony was brought up ; in other cases only the branches which had been marked were collected. The measurements made are recorded in the table on p. 214.

In all the colonies recovered a number of branches had undergone regeneration of greater or lesser amount. The total number of branches which we were able to measure was 144. In all these cases the branches were broken cleanly across at various, but never very great, distances from their tips, so that the regeneration was always of a simple type.

The information obtained from the experiment is well illustrated by the figures on Plate VIII. In Fig 1 is shown the tip of a branch of *Acropora formosa*. This branch had

been broken off seven weeks before the condition reached in the figure was attained. The broken end was still almost flat, but the flesh had healed across it, and the axial polyp had regenerated a new distal end, and was surrounded by a ring of very small subsidiary polyps; the calices of these are visible as dots in the photograph. Figs. 2-5 (*Acropora polymorpha*) show further stages in the process. In the branch shown in fig. 2 the regenerated portion had become a short cone, surmounted by the now well-developed calyx of the terminal polyp, with numerous small subsidiary calices on its sides.* The branch illustrated in fig. 3 had formed a much longer cone of new skeletal material, and the lateral calices were well developed; but the site of the fracture was still conspicuous. In the next branch the situation of the fracture had become less obvious because the regenerated branch had become relatively stout; and one of the lateral polyps had become prominent and had started a new branch (on the right-hand side in the figure). In the last branch of the series (fig. 5) the regenerated part had become very well developed, and it occupies most of the figure. The point of fracture was by this time only just distinguishable, and the regenerated portion had become definitely trifid.

The general principle of the process of regeneration just described holds good for all the species of *Acropora* used in the experiment; but the details differ from one species to another. The new growth is always started by a regenerated terminal polyp, and is led by this polyp throughout. Lateral polyps appear on the sides of the regenerating cone, and when this cone subdivides into branchlets, each branchlet is headed by a terminal polyp which has been derived from one of the lateral ones. The differences of detail which supervene may be traced to the exact shape of the terminal calyx which is regenerated; to the form of the lateral calices; to the extent to which they project beyond the general surface of the branch; and to the form of that portion of the branch which lies below the fracture. Some of the varied appearances produced in the several species are illustrated in the later figures on Plate VIII. In figs. 6 (central branch) and 7 the new growth has the form of a narrow, chimney-like extension of the old branch; in fig. 8, which includes three regenerating tips, the broad shape of the new terminal calyx results in the production of a low rounded cone.

Apart from the details of the regenerative process, the experiment demonstrated a very curious fact, which again is illustrated by Plate VIII. All the branches shown in figs. 2-5 belonged to a single colony; they were all broken on the same day; and they all regenerated for the same length of time. Yet the amounts of regeneration attained by them were very different. Altogether thirteen branches were recovered from this particular colony, and the amount of regeneration varied among them from 4.0 mm. in the least active to 38.75 mm. in the most active, with all grades between (see table on p. 214). The amount of regeneration achieved by the most active branch, therefore, in the same time, was nearly ten times that achieved by the least active. The colony was perfectly healthy at the end of the experiment, and there was no indication that any of the branches were less healthy than others. On the contrary, our general experience with regenerating corals, throughout the year, would lead us to suppose that in many species such irregularity is perfectly normal and usual. This conclusion is supported by other

* In this figure there may also be seen a diagonal ridge on the part of the branch situated below the site of the fracture; this ridge was formed by an overgrowth of the tissue and skeleton of the coral round the silver wire which marked the branch. The wire was completely embedded in the part shown. This is a frequent occurrence in marked corals.

colonies in this particular experiment, and similar results have been recorded from Cocos-Keeling Islands by Wood-Jones, who also describes the dominance of the terminal polyp in regeneration, and the variations in the development of a branch which may occur according to whether or not the terminal polyp is prevented, by the nature of an injury, from regenerating ('Coral and Atolls,' 1910, pp. 69, 82, 111, etc.).

Is there any connection between irregularity of regeneration and the general growth-form of the colony? We cannot answer this definitely from the experiment, but we think that it might be possible to demonstrate such a connection. In the case cited above (*Acropora polymorpha*) the colony was one of straggling stagshorn growth, with no particular general form, such as would naturally be produced by irregularities either of regeneration or of ordinary growth. There are other species, however (for instance *A. squamosa*, Plate I, fig. 6), in which the adult colony forms a dish-like or shelf-like structure



TEXT-FIG. 4.—Diagram illustrating the change of form which took place in a small colony of *Pocillopora* during a period of 31 weeks. The details are described on p. 188. The shape of the colony at the beginning of the experiment is indicated in solid black; its shape at the end, in outline. The branch A (stippled) died after making the amount of growth shown. The diagram is slightly larger than natural size.

with a stem underneath or at one side. In such a case the branches which spring from the upper surface of the expansion tend to be neatly arranged, and their tips attain a fairly even common level; and it might be expected that during regeneration they would grow new tips at a fairly even rate. Unfortunately our results include no clear case of this description; but the nearest approach to it is shown by colonies 4 and 5. These were colonies of *Acropora gemmifera* (Plate IX, fig. 1), in which there was some approach to a general surface-level in the tips of the branches (though less definitely than in *A. squamosa*);

and here the amounts of regeneration shown were more regular than in *Acropora polymorpha*, though even here the maximum new growth was two or three times the minimum (but this is much less than ten times). *Acropora formosa* is one of the stagshorn species, and the irregularity which it exhibits is therefore in order. In *Acropora quelchi* the results should be fairly regular, whereas the measurements made reveal considerable irregularity. This is more apparent on paper than in fact (all the amounts being small); in a colony which was collected entire (No. 6), the regenerating branches had their tips at a fairly even level, much as in the photograph of *A. gemmifera* on Plate IX, fig. 1.

Before leaving the question of regeneration we may add certain data on the subject which may be gleaned from Experiments I and II.

In Experiment I, No. 40b, *Acropora quelchi*, a compound branch was accidentally broken off near its base, at the beginning of the experiment. Twelve weeks afterwards this branch had regenerated about half an inch; by the end of the experiment (30 weeks after the breakage) it was not certainly distinguishable from the other branches, and its total growth could therefore not be accurately determined. Whatever its exact growth, however, this branch and the neighbouring ones between them had filled in the gap in the outline of the colony left by the breakage, and had restored its proper symmetry.

In Experiment II, No. A4, *Pocillopora bulbosa*, the original colony had been halved so neatly that one of the halves (A4) was almost flat on one side. By the end of the experiment new branches had appeared on the flat side, and had become very well formed, so that the shape of the whole colony had become normal once more. This colony is illustrated in Plate VII, figs. 3 and 4, and also in Text-fig. 4. The text-figure was constructed by superimposing tracings made from the photographs taken at the beginning and end of the experiment; it was possible to do this accurately by reference to fixed marks which were the same in both photographs. From this figure it may be seen (1) that the branches on the uninjured side have continued to grow actively; (2) that the branch labelled "A" died after making a little growth; and (3) that a series of new branches has been formed on the broken side. Unfortunately the latter branches were foreshortened in the photograph, whereas the normal branches were recorded more in profile, so that the amount of growth in the new branches is minimized in the text-figure; but it may be seen from the plate that their growth was of considerable amount.

EXPERIMENT IV.

(*The Growth of Corals Derived from Planulae which settled on Material Planted Out on the Reef.*)

One of our earliest activities on the reef was to fix in various places on its surface collections of clean material, upon which we hoped that coral planulae would settle. The materials used were logs of wood, pieces of clean beach-sandstone which had not been attacked by organisms, short lengths of earthenware drainpipe, glass jars fixed in wooden crates and the cleaned shells of clams. These objects were fastened down by means of several devices, so that they could not shift, and were placed in a variety of habitats. In this experiment the date on which the materials were fastened down is known, and also the date upon which young corals were collected from them; but the dates

upon which planulae actually settled are, of course, unknown, so that the age of any young colony can only be stated as something not exceeding, and usually *less than*, the period of the experiment.

The variety of animals which attached themselves to these materials was not very great. The materials were left untouched, for the most part, for nearly eleven months; during this time a good deal of fine sediment was deposited upon and among them, and this appeared to interfere somewhat with their colonization by animals. The algal succession was interesting, more especially during the first few weeks, when a growth of microphytic forms sprang up on the surface of most of the materials.* Later on some of the materials became clothed by a strong growth of *Padina*. We feared that the early coating of algae and sediment might prevent any corals from settling at all; but by the end of the experiment about 40 young colonies had become established. Thirty-six of these were collected without damage, and their sizes, at the end of the experiment, are recorded in the Table on p. 215.

Of the 36 colonies recovered, 26 belong to the common moat-dwelling species *Pocillopora bulbosa*. This coral seems to establish itself under such circumstances more readily than any other. This is borne out by the fact that if one wishes to obtain a series of very young colonies the best places to visit are the "gaps" (actually regions of low level, not actual interruptions) in the rampart, through which water streams out after the sea itself has deserted the flat, on the ebb tide; and through which it streams once more, on the flow, before the whole flat is inundated. In one of these gaps, in 1929, a large number of young *Pocilloporae* had managed to establish themselves, the planulae presumably being left behind by the streaming water in angular crevices of the shingle. Young colonies of *Acropora* were also frequent here, but *Pocillopora* predominated.

The young *Pocilloporae* which had grown on our clean materials were of very different sizes, no doubt partly because they had settled at various times throughout the 11-month period. The largest colonies had formed well-developed small sheets of polyps, with diameters such as 11.0×10.0 mm., 10.4×7.7 mm., and 14.5×9.5 mm. In 14 of them the first vertical branch had appeared. In some of these the branch is still in an incipient condition, forming simply a hump on the basal expansion. In the more advanced specimens it has become a definite branch, and in one of them (No. 14) it has become trifid at the tip.

Apart from the *Pocilloporae*, we obtained 7 colonies of *Porites*, 1 of *Cyphastrea*, and 2 of an undetermined coral, perhaps also a *Poritid*. The largest colonies of *Porites* were 7.0×6.0 mm. and 12.0×6.5 mm., and this size they attained in twenty-seven weeks.

The experiment therefore established the following points:

(1) *Pocillopora bulbosa* will settle readily in the moats at Low Isles, and may form an expansion measuring as much as 11.0×10.0 or 14.5×9.5 mm. in less than eleven months. It may also form a trifid branch during this period.

(2) *Porites* may attain sizes such as 7.0×6.0 or 12.0×6.5 mm. in twenty-seven weeks or less, in the Low Isles moats.

Certain other animals settled on the materials, as well as corals, and the largest of these were also measured at the end of the experiment. In a box of materials planted in the anchorage there were found two colonies of the interesting polyzoan *Retepora graeffei*,

* Some details of the algal succession will be provided by G. Tandy in the systematic report on the algae.

which had attained heights of 21.0 mm. and 13.0 mm. respectively (forty-three weeks or less). An organism, which grows very rapidly in the moats is the sponge *Gellius fibulatus*, with which is combined an alga. The organism forms straggling green branches, which may attain lengths of 100 mm., 105 mm., etc., in a period of sixteen weeks. Oysters of several species also settled on the materials, and the sizes of these are recorded on p. 215. Vermetids had also settled, and attained diameters up to 12.8 mm. during the experiment.

BUDDING IN ASTRAEID CORALS.

The question of asexual reproduction among the Madreporaria is one of considerable interest. It is a question about which much has been written, but about which the sum of our actual knowledge is still quite limited. In the early days two processes (budding and fission) were assumed to take place from a study of the skeleton; and even when a study of the soft parts was undertaken, notably by Duerden, the idea of the prevalence of these two processes remained. Duerden, in his monograph on the West Indian Madreporarian polyps (1902, p. 497), remarks: "Although the stages in division of the mouth or stomodæum have not been actually observed, the results to be detailed below prove conclusively that in fission the stomodaeal wall is actually divided into two equal or unequal parts," etc. In spite of this conclusion, the tendency of recent work has been all in the other direction. Matthai, in his paper on asexual reproduction in the Astreaeidae (1926), claims quite fairly that in the species which he studied the process of stomodaeal fission does not exist at all; and further, that there is as yet no evidence of its occurrence in any Madreporaria. Matthai therefore substitutes for "fission" and "budding" a distinction between two varieties of budding, (a) *extra-tentacular budding*, in which a new polyp appears from tissue lying outside the tentacular crown of any existing polyp; and (b) *intra-tentacular budding*, in which a new mouth arises on the peristome of an existing polyp, inside its circlet of tentacles, in correlation with an extension of the peripheral part of this polyp; followed in some cases by a gradual separation of the new part from the old. More polyps than one may arise simultaneously in this way. This process is the "fission" of earlier authors, but it involves in fact the creation *de novo* of a mouth and throat from tissue belonging to or lying below the peristome, without any subdivision of an existing mouth or stomodaeum; preceded and accompanied by gradual extension and modification of form in the surrounding parts, but not by any process of rupture. Matthai's conclusions, like Duerden's, are based primarily upon a study of serial sections; neither author has seen the processes described take place in the living animal. In spite of this, Matthai has, to our way of thinking, demonstrated his case for the Astreaeids; and we hoped whilst in Australia to supply observation of living polyps which would confirm his work. It proved impracticable, in view of precedence of other work, to observe any given colony continuously, except in the cases of young *Pocillopora* and *Porites* (neither of them Astreaeids), in which the method of extra-tentacular budding was observed in detail and has already been described (Vol. III, No. 3 of these reports); but a few data referring to Astreaeids in which intra-tentacular budding takes place were also obtained, and these are presented here. Although they do not include direct observation of the *de novo* formation of new mouths, they do include the record of a formation of new mouths which can hardly have taken place in any other way. They fall into line very well with

Matthai's conclusions; and we saw nothing at any time which would suggest that subdivision of an existing mouth or throat ever occurs. In this respect the Madreporaria contrast with the Actinians, in which fission of a sudden description, involving rupture of both body-wall and stomodaeum, has been fully observed in living animals (Stephenson, 1929). Matthai's statements must also be modified to this extent—that fission, including subdivision of the throat, has been directly observed by Evans in *Corynactis*, which, according to our view of Anthozoan relationships, must be classified, not as an anemone, but as an aberrant madreporarian which produces no skeleton.



TEXT-FIG. 5.—Increase of polyps in *Favia*; no. 70. See text, p. 191. The red lines indicate the outline of the whole colony, and also the outlines of the calices of individual polyps, at the beginning of the experiment; the black lines indicate the same features some months later. In the centre of the figure the new and old outlines of the polyps are more or less coincident; as the edges are approached the new outline becomes more and more peripheral to the old one.

SUBDIVISION OF POLYPS IN FAVIA.—A number of the colonies used in Experiment I belonged to the genus *Favia*. In several of these the photographs taken at the beginning and end of the experiment showed clearly what had happened to individual polyps in the interval. One of these pairs of photographs is reproduced on Plate VI, figs. 1 and 2, from which the clarity of the evidence produced may be seen. In the case of five colonies the changes were worked out in detail, and are summarized in the following table: and to these are added details of a sixth small colony on which observations were made direct. In making the counts from photographs only the polyps in the central parts of each colony were used, since those round the edges were represented at angles which made them unsuitable for observation.



TEXT-FIGS. 6 AND 7.—Increase of polyps in *Favia*; nos. 80a (above) and 48b. See text, p. 191.
Conventions as in Text-fig. 5.

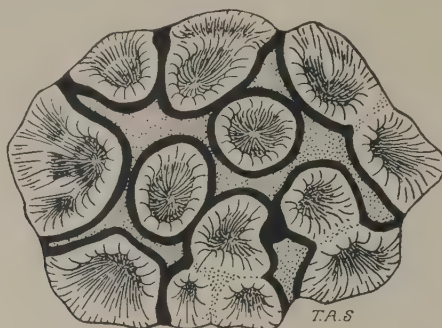
The changes which took place in the colonies in question are represented graphically in Text-figs 5 to 10. From the table it will be evident that the 259 polyps counted at the beginning of the experiment had become 394 by the end of it; that of the original 259, more than half were still undivided at the end, though many of these had altered in shape



TEXT-FIGS. 8 AND 9.—Increase of polyps in *Favia*; nos. 81b (above) and 2a. See text, p. 191.
Conventions as in Text-fig. 5.

as one of the preliminaries to subdivision; that of the remainder, a high majority had divided into two, a considerable number into three, and a very few (six only) into more than three, the maximum being reached in the case of a single polyp which became transformed into six new ones. (In the wording of the last sentence, as in the table, it is assumed that the process of multiplication of polyps was one of intra-tentacular budding in every case; it is possible that in a certain proportion of cases new polyps had arisen by the extra-tentacular method; but if so these would be quite in a minority.) We do not wish to express any opinion as to the details of the process by which these new polyps arose

(a matter dealt with fully by Matthai), but would point out that in the cases where more than three polyps were present at the end of the experiment, in the space previously occupied by one, these may have been produced by abnormal means, or by successive processes; they need not necessarily have arisen by a single multiple subdivision.



TEXT-FIG. 10.—Increase of polyps in *Favia*; no. 92a. This figure represents diagrammatically the appearance of a young colony at the end of the experiment, but the recent developments which have taken place in the several polyps are indicated by thick black lines. Each polyp, or group of 2 to 3 polyps, enclosed in a black line, was represented by a single polyp at the beginning of the experiment. Of the 9 original polyps, 4 have become definitely subdivided, and one of the remaining 5 is well on the way to becoming three. The coenosarc between the contracted polyps is stippled. About twice natural size.

Increase of Polyps in Favia.

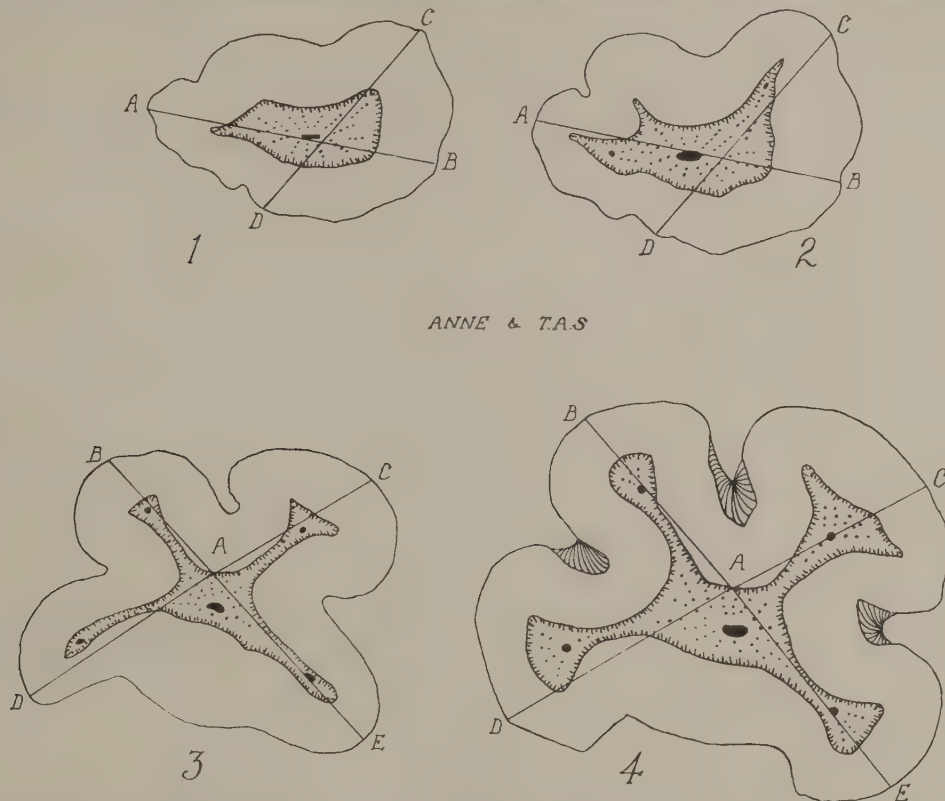
Reference No.	Name of coral.	Period of experiment.		Number of polyps examined	Number which remained undivided.	Number which became 2.	Number which became 3.	Number which became 4.	Number which became 5.	Number which became 6.
		Weeks.	Days.							
48b	<i>Favia doreyensis</i>	33	0	50	34	12	3	1		
80a	„ „	31	2	41	16	19	5	1		
70	„ „	33	1	114	91	21	2			
2a	„ <i>favus</i>	31	1	20	7	12	1			
81b	„ <i>doreyensis</i>	31	2	25	5	10	6	1	2	1
92a	„ sp.	26	5	9	5	3	1			
Totals for the six colonies .				259	158	77	18	3	2	1

It may be noted that the increase in the number of polyps, in a period of about eight months or less, was surprisingly great, considering the massive nature of the colonies and their relatively slow rate of growth. In these *Faviae*, however, the history of the mouths could not be followed.

SUBDIVISION OF POLYPS IN LOBOPHYLLIA. In several of the colonies of *Lobophyllia* used for Experiment I, detailed maps and measurements of the colonies were made at the beginning of the experiment, in the hope that the development of each colony might be followed out. Six of these colonies survived the experiment, and were again mapped

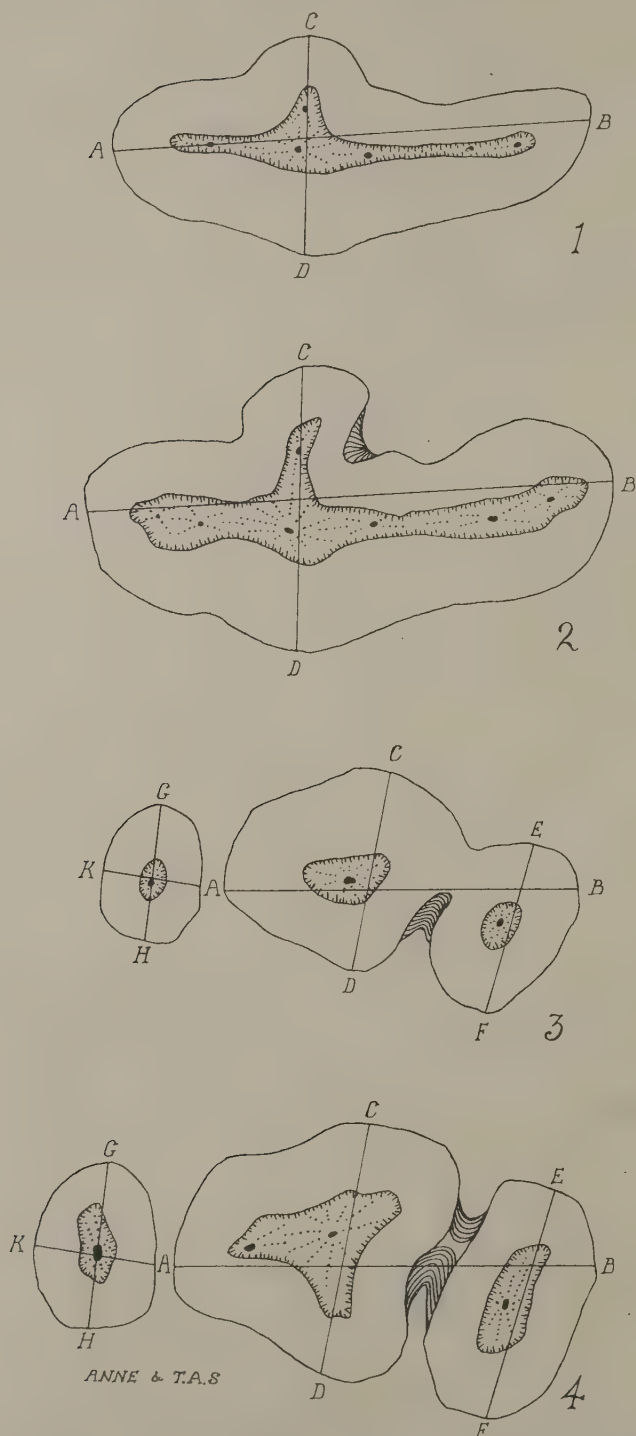
and measured afterwards. These colonies provided the details summarized in the following table, and represented in Text-figs. 11–14.

In the case of these *Lobophyllia* the change which took place in the colonies during a period of about seven months was less marked than in the case of *Favia*. This is to be

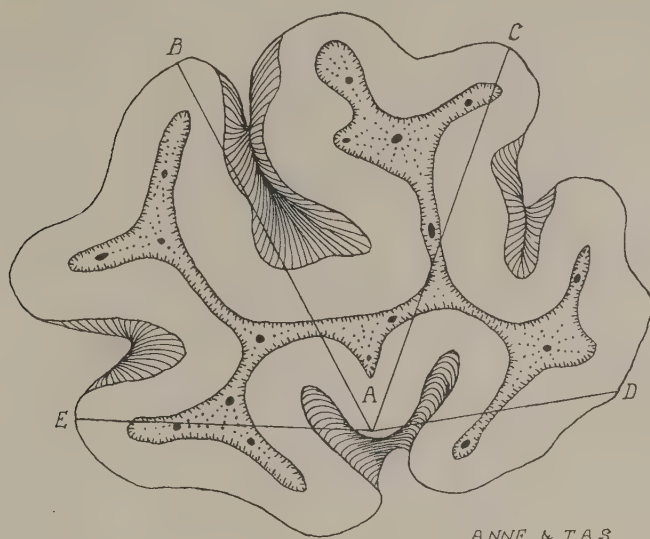


TEXT-FIG. 11.—Development of polyps in *Lobophyllia*. The lengths of the diameters indicated by straight lines are given in the table on p. 199. The figures are purely diagrammatic, but are drawn to scale, so that the increase in size as well as the development in shape is represented; but the corals are curved, and have to be represented in the diagrams as flat. Figs. 1 and 2 represent the same coral (no. 54a) before and after the experiment; Figs 3 and 4 represent another coral (no. 53a) in the same way. The mouths are black, the peristomes stippled; the line surrounding each peristome represents the margin of the column wall, drawn in over the retracted tentacles; the upper part of the column wall, which covers the outer parts of the septa, is unshaded; and the outer wall of the colony, covered by the tissues of the edge-zone (where visible), is shaded with lines. The changes represented in this and the succeeding figures are described on pp. 194–9.

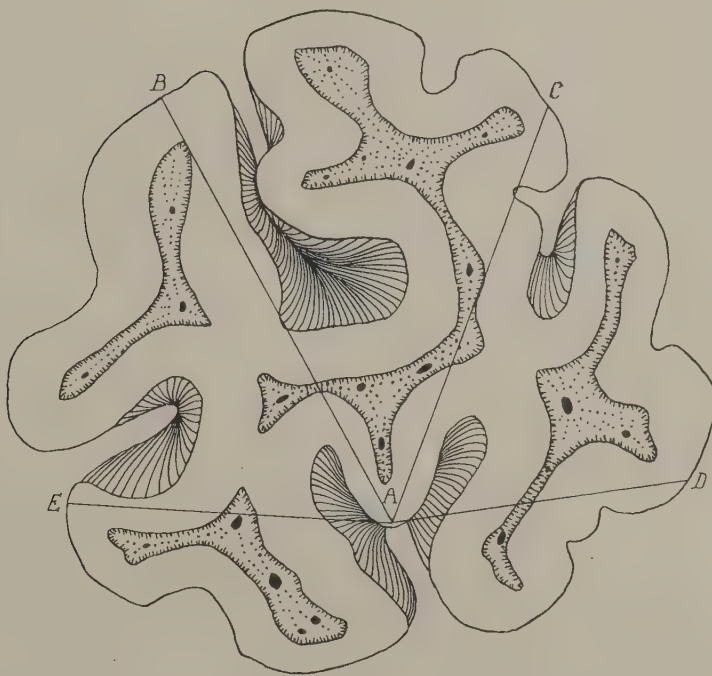
expected, since the polyps of *Lobophyllia* are very much larger than those of *Favia*, and are also more or less meandrine—that is to say, do not so readily subdivide. The actual number of polyps only increased from 12 to 16 in the time; but apart from this there was an appreciable extension and development of the sinuous shapes of the polyps, in all the colonies, as may be seen from the text-figures. In addition to this, the polyps studied started by having forty-seven mouths among them, and ended up with fifty-nine, *i. e.* twelve new mouths had come into being during the experiment. Now it is true that the



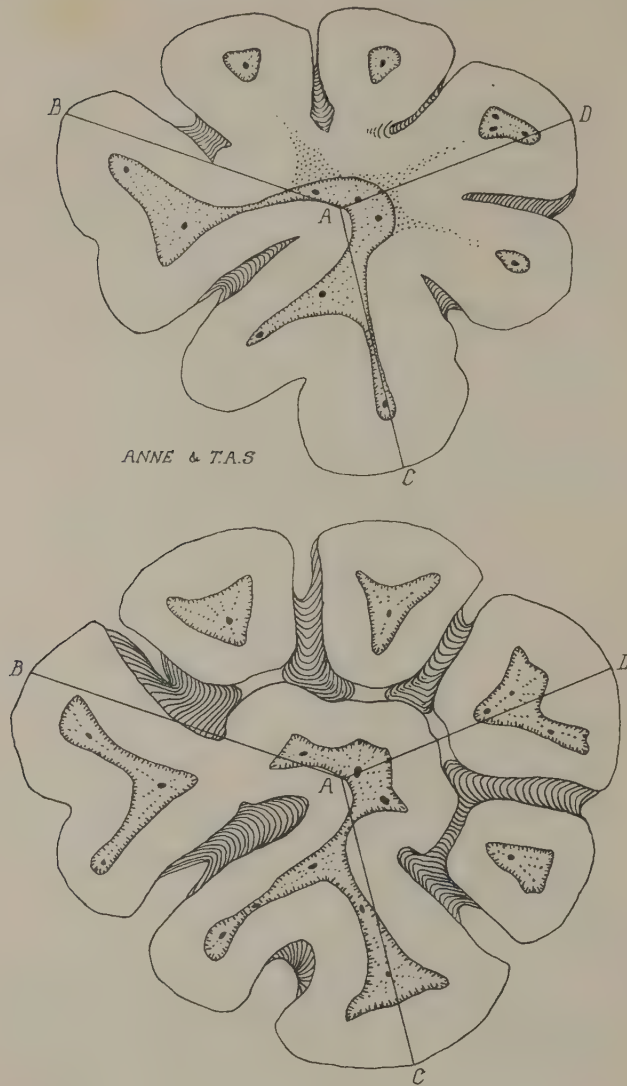
TEXT-FIG. 12.—Development in polyps of *Lobophyllia*. 1 and 2, no. 92e before and after the experiment; 3 and 4, no. 92d, before and after the experiment. Conventions as in Text-fig. 11.



ANNE & T.A.S



TEXT-FIG. 13.—Development in polyps of *Lobophyllia*. No. 53b before and after the experiment.
Conventions as in Text-fig. 11.



ANNE & T.A.S

TEXT-FIG. 14.—Development in polyps of *Lobophyllia*. No. 54b before and after the experiment. Conventions as in Text-fig. 11, except that in the upper figure there is some close stippling on the upper part of the column wall, indicating the remains of an earlier stage of development. The peristomes of the three polyps with which this stippling is connected have become distinct from the principal peristome of the colony, but their peripheral tissues are still in continuity with those of the large polyp. In the lower figure the smaller polyps have become distinct, but in three of them a little bridge of edge-zone, left white in the figure, still links them slightly to their parents. In the smallest polyp even this bridge has been lost.

Development in Polyps of Lobophyllia.

Reference No.	Period of experiment.		Measurements in centimetres.		Number of polyps at beginning of experiment.	Number of polyps at end of experiment.	Number of mouths at beginning of experiment.	Number of mouths at end of experiment.
	Weeks.	Days.	Original measurements.	Increase.				
53a	29	5	AB 2.3	1.0	1	1	5	5
			AC 2.7	0.5				
			AD 3.25	0.7				
			AE 3.32	0.48				
53b	29	5	AB 6.22	0.94	1	4	17	23
			AC 6.07	0.53				
			AD 3.74	0.75				
			AE 4.39	0.43				
54a	29	5	AB 4.35	0.28	1	1	1	3
			CD 3.55	0.44				
54b	29	5	AB 4.5	0.62	5	6	15	17
			AC 4.15	0.45				
			AD 3.9	0.65				
92d	26	5	AB 5.54	1.04	3	3	3	4
			CD 3.16	0.78				
			EF 2.72	1.0				
			GH 2.15	0.44				
92e	26	5	KA 1.52	0.4	1	1	6	7
			AB 7.46	0.74				
			CD 3.42	0.98				
Totals	.	.	.	.	12	16	47	59

All six specimens came from and were kept in the Anchorage. Nos. 92d and 92e were pieces from large colonies; the remainder were complete young colonies. The distances measured on the colonies are indicated in Text-figs. 11-14. More than one species is represented, but identification of young colonies is very difficult.

actual birth of these new mouths was not witnessed by anyone; but some of them were situated, at the end of the experiment, in places which they could not have reached without having actually moved a considerable distance across the peristome, if they were derived by fission from pre-existing mouths. There seems to us to be no doubt that they arose *de novo* and *in situ*, and that migration from the site of another mouth is out of the question. This is particularly well brought out by Text-fig. 11, figs. 1 and 2, in which the polyp began with one mouth and ended with three; and the two new ones are situated at distances of 9.0 and 13.5 mm. respectively from the old one. If these new mouths had arisen from the single original mouth, they would have had to migrate across distances of *pre-existing* peristome comparable to their distances from the old mouth at the end of the experiment; but, although the interval between two adjacent mouths can and does increase as the polyp grows (by interstitial growth of the intervening tissue), there is no reason to suppose that the newly-formed mouths, in a case such as this, have performed, across tissue already in existence, a migration of the magnitude demanded by the supposition that they arose from the original central mouth. The distances which separate new mouths from old ones in the other colonies studied also support this conclusion.

THE RELATION BETWEEN FORM AND ENVIRONMENT IN CORALS.

By T. A. STEPHENSON.

Among the discussions which have been written on this subject, one of the most notable is that of F. Wood-Jones, in 'Coral and Atolls' (1910)*. Before proceeding to Australia some of us read this account with great interest, and it fell in so well with our expectations and appeared so soundly based, that we were inclined to take it for granted that our work would tend to confirm the author's views. As the year progressed, however, we found that some modification of these views seemed necessary; but although we are obliged to dissent in certain respects from the well-known views expressed in 'Coral and Atolls,' we should like to acknowledge the stimulus which we received from that most valuable work. Our object in criticizing Wood-Jones's conclusions is not destructive, but aims at advancing our knowledge of the problem of species among corals by modifying a theory which, though undoubtedly true in its broad outlines, is probably mistaken in its detailed applications.

The gist of Wood-Jones's argument, if I understand it rightly (and many of his statements are so definite that there seems to be little room for misunderstanding), is that there are in reality far fewer species of coral than the systematic literature would lead one to suppose†; and that the effects of environment are paramount in determining the shape, and even the details of texture, which a colony will assume.

Now up to a point I agree with this entirely. The identification of an isolated colony or fragment of coral, the circumstances of whose life are unknown, by anyone who is unfamiliar with the reef from which it came, is sometimes quite possible; but in many cases it is so difficult that it may, without exaggeration, be described as an impossibility. The result of this has undoubtedly been the creation by systematic workers of many "species" which would be found, if they could be studied more fully, to be nothing more than growth-forms of one another. I also admit freely—and the fact is very important—that environment influences growth-form in corals.

On the other hand, I feel equally definitely that Wood-Jones has represented his case a good deal too strongly, and that he has exaggerated the influence of environment very much; and that, although he is right in thinking that there are fewer coral species than the literature would lead us to suppose, he nevertheless very much underrates their number.

Even though there may, in fact, be nothing more than a difference of degree between our views and those of Wood-Jones, I suspect that the effect of his work, together with the general difficulties of coral systematics, has been to leave in the minds of a number of people the question: "Are there species among corals at all?" Since this question is one of very considerable interest, and one which, if solved, will advance our knowledge of natural processes very greatly, I feel that a discussion of Wood-Jones's views in the light of new evidence is justified. Before commenting on them in any detail, therefore, I will

* First issued in 1910, re-issued in 1912.

† That some of our most experienced systematic workers would agree with this opinion is evidenced by such remarks as the following (Vaughan, 1918, p. 161): "It is not practicable here to review the species of *Acropora* reported from the Great Barrier Reef, as such a task is probably not possible without a critical study of Brook's types and of the other specimens examined by him. However, I will say that I doubt if half as many species as he recognized will be found valid."

present a short account of the distribution of forms of growth upon Yonge Reef, a reef belonging to the Outer Barrier series which is exposed to strong surf from the open Pacific.

With Wood-Jones's views in mind I asked Dr. E. A. Fraser, during our visits to the reef, if she would examine the distribution of corals upon it with the express purpose of finding out whether their distribution accorded with the ideas of Wood-Jones: if she would also collect a series of specimens illustrating her conclusions. The resulting notes and collections made it possible for me to write the following paragraphs with some backing for my view, and I am much indebted to Dr. Fraser for the assistance thus provided. I myself kept this investigation in mind when examining the reef, and came to the same conclusion as Dr. Fraser: and a summary of the notes, to which we both agreed, was written at the time. The result of these observations may be expressed as follows (the terms used in connection with Yonge Reef may be understood by reference to Vol. III, No. 2 of these reports, in which the reef is described):

Collections of corals were made, and notes were taken, in each of the four zones of the reef which lie nearest to the position occupied by the breakers at low water of low spring tides.* these zones being successively (starting at the edge of the reef nearest the breakers) the outer ridge, the outer moat, the reef crest and the inner moat. On the outer ridge one stands a few yards only from the point at which the waves actually curl over and break: and the ridge is even then constantly washed by the surge of the waves beyond their breaking-point. The outer moat is also much swept by this surge. The reef-crest rises entirely above the sea at low spring tides, but has pools on its surface; and the inner moat forms a series of pools, which at such times are relatively quiet.

In the first place the growth of coral at and near the seaward edge of the reef is often rich and varied. This is apparently in contrast to the state of affairs on some atolls, among which is Cocos Atoll. "In that area on which the surf beats—the seaward edge of the barrier—living coral growth reaches its minimum of individuals as well as of species" ('Coral and Atolls,' p. 159).

Secondly, on the outer ridge and in the outer moat many of the colonies of *Acropora* have short stumpy branches, and forms with very solid conical branches are common; but there exist in addition many large bracket-like growths made up of delicate branches. It is true that the basal parts of the branches are very stout and anastomosing, and the terminal branches short; but the latter are very easily broken. Further, one of the most delicate of all the species of *Acropora*, *A. delicatula*, occurs in this wave-swept region, and is common, among other places, on the sides of fissures in the outer ridge; and this coral is so breakable that it is very difficult to collect an intact specimen of it, the least tap with a chisel being enough to break any of its branches. On the contrary, large or straggling stagshorn corals naturally do not occur in the wave-zone, since they would be torn up; though a heavy stagshorn with creeping branches (*A. decipiens*) is common.

On the reef crest the selection of species is somewhat modified, probably partly by the fact that many of the colonies which grow there are fully exposed at low water of low spring tides. Common forms here are strong tuft-like colonies of *Acropora gemmifera* (with short stout branches) and *A. squamosa*; but the breakable stagshorns *A. hebes*

* This account of Yonge Reef describes only the state of affairs which prevails at low water of low spring tides, since we were unable to visit the Reef at other times. In writing the discussion, however, allowance has been made for the fact that the conditions vary with the rise and fall of the tide.

and *A. pulchra* also occur. This reef crest is decidedly bare in some places, but quite well populated in others.

In the inner moat all the main growth-forms mentioned for the outer ridge and moat are also to be found. It is not until the "anchorage coral zone" is reached that any profuse growth of straggling forms is present; and by this time we are definitely on the leeward side of the reef. But even here there is the somewhat contradictory feature that forms of *Acropora gemmifera* with distinctly short, solid, conical branches are common on coral heads to leeward of the reef, half a mile or more from the low-water position of the breakers.

This means, then, that apart from tall stagshorns, any of the principal growth-forms of *Acropora* may be characteristic both of the outer ridge and of the regions behind it. This statement need only be qualified to this extent—that on the outer ridge the stumpiest forms are probably at their most plentiful, and are often present in their most exaggerated degree.

I feel that the account just given does not altogether coincide with the view, which has by now become somewhat stereotyped, of a somewhat mechanical differentiation of growth-forms according to the local variations of an all-powerful environment. On Yonge Reef there exists, it is true, a great array of squat forms near the breakers—forms so solid that it is hard work to detach them even with a strong cold chisel; but against this we have to set the fact that in this same environment there occurs the delicate *A. delicatula*.* flourishing perfectly well; and the further fact that the heavy forms persist to leeward of the reef, though possibly in a less extreme form. Also, the reef crest, which must be considerably wave-swept at some states of the tide, bears a certain amount of actual stagshorn coral, though not of the most straggling types. This account follows the traditional one only in so far as we agree that large and straggling stagshorn types cannot occur in the wave zone; and conversely that low-growing forms are characteristic of this zone.

Some of the points just mentioned, together with further ones, are illustrated in Plates IX and X. In Plate IX, fig. 3, we see the extreme of reduction of the branches of a species of *Acropora* (probably *A. gemmifera*) to short cones (this photograph was taken near the outer ridge); in fig. 4 a colony of *A. gemmifera* from the leeward side of the reef, in which the branches in the centre are still very short and stumpy. In Plate III, figs. 3 and 4, and Plate X, fig. 5, are seen intermediate conditions of the same species, and in Plate IX, fig. 1, a colony of it from sheltered water at Low Isles. The type of variation which may legitimately be expected† within the limits of a single genuine species is illustrated by this series; the effect of environment is there, but is correlated only in a general way,

* Matthai identifies this species as *A. delicatula*, in which case our specimens are presumably young colonies of a species which ultimately becomes bracket-like. It is a possibility, however, that our examples are in reality adult; but only another visit to the reef could settle the point.

† I am aware that by reproducing photographs of several specimens of a single species (especially in the case of *A. gemmifera*) I am laying myself open to the criticism that, in the opinion of a given systematist, my photographs represent, not one species, but several. Such differences of opinion are inevitable in work dealing with the species in difficult genera. In these cases I have consulted the systematic literature carefully, and feel that there is good ground for my view. It may be noted in this connection that weight should be given to the experience of the field-worker who has seen the species growing in its hundreds, as well as to the opinion of the purely systematic worker. With reference to the present figures, even if they did not all represent *A. gemmifera*, *sensu stricto*, they would still illustrate "the type of variation which may legitimately be expected within the limits of a single genuine species."

and not in detail, with the form of the coral; specimens almost exactly like Plate IX, fig. 1, could be procured on the same coral head as the one shown in fig. 4, and moreover, stumpier forms are to be found in the Low Isles anchorage (one of the most sheltered parts of a sheltered reef), as is witnessed by Plate III, figs. 3 and 4. Next, in fig. 7 on Plate X we have the aforementioned *Acropora delicatula* from the outer moat. This has the wrong characteristics for a rough-water coral, measured by the Wood-Jones criteria; instead of a dense compact structure, with corallites flush with the surface, it has slender breakable branches, which have prominent lateral corallites. Again, Plate X, figs. 6 and 8, show two examples of *A. hyacinthus*, one from the most sheltered part of Low Isles, the other from the outer ridge of Yonge Reef; there is certainly a difference between them—a thickening up of the breaker-zone specimen; but the difference is by no means of the magnitude which should be expected according to the Wood-Jones view (see below). Lastly, in figs. 1 and 2 on Plate X we have an example of a fairly frequent occurrence, which is definitely against an environmental interpretation. In fig. 1 we have a fairly normal branch of *Acropora squamosa*; in fig. 2 a totally different one, which could easily be identified as belonging to a different species; yet both specimens belonged to one and the same colony. The transition from branches of one type to branches of a different build is also shown in the case of another species, in Plate IX, fig. 4. The case of figs. 1 and 2 cannot be dismissed simply as the effect of the regeneration of a new type of branch on an injured colony; it is to all appearance an example of actual variation, within the same colony, having no connection with environmental effects.

It is now possible to examine some of the conclusions of Wood-Jones more closely; and this will be done most conveniently by quoting passages from 'Coral and Atolls,' and commenting upon each in turn:

1. "From the study of the life of the colony in different surroundings, and from the repair of injury, and death, in unsuitable habitats, I think it will be seen that the number of the true species of corals is by no means so great as is at present supposed. There is no doubt that a great number of our museum-made species are mere vegetative varieties, produced in response to the demands of the environment" (p. 131).

With much of this I agree entirely.

2. "though a definite inherent growth tendency is strongly implanted in the embryo, still the demands of the environment may call forth *any type of vegetative growth*" (p. 72; italics mine).

This statement certainly needs modification. The environment cannot call forth "any type of vegetative growth"; it can merely induce certain variations, within definite limits; and although the "inherent growth tendency" is admitted in the quotation, it is in fact given comparatively little weight in the book, whereas it is in reality very important.

3. "Totally different forms are produced in totally different environments, but these forms must not be regarded as "species," for they are mere variations of vegetative growths in response to the necessities of the life-surroundings of the colony" (p. 93).

This is justified if understood in the light of the modification introduced under no. 2, but hardly, as we shall see, in the degree in which it was intended by its author.

4. "The rough-water forms of the *Madrepora* are highly characteristic, and all depend on the processes which always occur in this group when the "dominant apical zooid" is injured" (p. 88). "all these rough-water forms are in reality the result of perpetual injury" (p. 87).

There is no evidence in favour of these statements, and our work definitely points the other way. Wood-Jones has shown, it is true, that if terminal polyps are injured (and especially when the damage affects a large area of a branch), branching from lower down is stimulated; but it is not simply a repetition of such processes which produces the squat forms of rough water. A sufficient number of successive injuries to apical polyps would undoubtedly produce a curious colony, probably highly branched, and possibly with many of the branches incipient rather than properly developed; but the aspect of such a colony would not be the same as that of a normally produced stumpy colony, or if it were, the resemblance would be secondary and accidental. There appears to me to be no doubt that the ordinary squat, but often beautifully symmetrical forms of rough water are the result of the working together of two influences, (1) an inherent tendency to a certain degree of squatness, and (2) the gradual and normal growth of the colony under the action of the surf. This latter factor appears constantly to inhibit and hold in check the growth of the coral, with the result that the growth is restrained instead of exuberant, and results in compact instead of straggling forms of growth. As we have seen, however, such forms need not necessarily be of strong or massive texture, nor are massively branched forms by any means confined to rough water.

5. "it is diagnostic of a rough-water coral that its structure is compact and dense, and its corallites tend to be flush with the general surface of the growth" (p. 90).

This remark is expressed as a matter of tendency, and is therefore probably not intended to admit of no exception; but the exception provided by *Acropora delicatula* is such a striking one as to involve some modification even of a general statement. *A. delicatula* has a compact profile, certainly, and its branches are close-set, with a strong base; but its actual structure is not compact and dense, but light and breakable; and its corallites are decidedly of an angular and projecting type.

6. "In the smooth-water forms the predominant feature of the colony is the fragile nature of the growth." "Their branches are long and slender, their structure is far more porous, and their whole appearance is quite different from that of the colonies of the same species that chance to reside in wave-beaten areas" (p. 92).

These statements need modification to suit the facts that (1) solid massive forms (even of *Acropora*) are common in sheltered water (2) delicate fragile forms (though not with long branches) may occur in rough water.

7. "the actual structure of the coral depends greatly upon the presence, or absence, of sediment." "Sediment will alter the appearance of a coral more strikingly than any other influence" (p. 94).

Here, I think, as well as elsewhere in the book, Wood-Jones exaggerates the evil effects of sediment. That sediment can be, and is, harmful to a certain proportion of corals under certain circumstances I do not question. But the experiments carried out at Low Isles by Marshall and Orr (described in Vol. I, No. 5, of these reports) show clearly that many corals possess unexpectedly strong powers of ridding themselves of sediment, and that, in the ordinary circumstances of their lives, when there is usually (except in deep water) at least some water-movement to supplement the activity of their cilia, sediment cannot be considered as holding the dominant position, as a lethal factor, assigned to it by Wood-Jones. Its importance will vary with different species and with different individual colonies; but speaking generally, it cannot be included among the most important and detrimental factors to which corals are exposed, except perhaps on the mud-covered

deeper portions of the seaward slopes of certain reefs, and during the infancy of corals, when they may be less able to cope with it than later on. Further, the detailed effects on coral texture claimed by Wood-Jones as the effect of sediment are distinctly non-proven.

In connection with the *general* form of the colony, reference may be made to the historic question of the colonies with dead flattened tops which have so frequently been noticed on reefs. These are attributed by Wood-Jones largely to the action of sediment. Undoubtedly at Cocos Atoll their distribution appears to support this view. At Low Isles, on the contrary, where such colonies are also common, the great majority of them occur in shallow pools on the reef flat, and the general level of their dead tops is so nearly coincident with the level of low water (varying a little with species) that it seems self-evident that they are the result of the death of the upper surfaces of the colonies, consequent upon the projection of the latter above the surface during the period of low water. Wood-Jones maintains that exposure to sun and air does not as a rule kill corals; but this is not our experience. We saw on Yonge Reef (and this was during the cooler part of the year) many colonies which had undoubtedly been killed by exposure during a few days of low spring tides; the same thing was observed at Low Isles, after a spell of hot weather, though the numbers affected were smaller. It is possible to recognize such newly killed corals by their clean white colour; they remain in this condition for a few days only after death, and then become overgrown with algae and brown with sediment. The fact appears to be, that although many colonies do survive exposure for quite a long succession of periods of low water (extending in some cases over years) after they have begun to project above the surface, other colonies which are perhaps less hardy succumb more rapidly. That the exposure wins in the end and kills the projecting parts of all of them, in certain types of surface-pools, is demonstrated by the endless succession of flat-topped platforms in the Low Isles moats. This does not mean that flat-topped colonies are never the work of sediment; a proportion of them may be, and probably are, due to it; but many are due to other causes, among them exposure; and probably in shallow water damage due to wave-borne fragments (also postulated by Wood-Jones), resulting in colonization of the wound by algae, is of more importance than the effect of sediment itself.

8. "we cannot foretell that a young colony of *Pocillopora* will certainly be *P. brevicornis* and not *P. nobilis* for, depending on the conditions of its surroundings, it might chance to be either" (p. 103). "I do not doubt either that all the forms of *Pocillopora* which are found in the atoll are in reality one species" (p. 133).

Now many of the extracts given above appear eminently reasonable, and mostly require modification rather than refutation. But in the last two quotations we reach the root of the matter, for it is in the application of the general principle to particular cases that the author appears to me to be wide of the mark, and to reveal the degree to which he has overstressed the environmental influences. Wood-Jones interprets his results as meaning that (to take a single instance) the corals represented in his figs. 25, 26, 32 and 33 all belong to one species. I should maintain, on the contrary, that even allowing for the maximum possible variation due to environment, they differ from one another in ways which are not connected with the environment, and which indicate the presence of more than one species among them; and that the same applies in other examples.

It appears to me, in fact, that Wood-Jones's observations are of great value, but that his conclusions have been somewhat vitiated by two factors:

(1) The fact that the seaward part of the barrier at Cocos Atoll happens to possess a less varied population of coral than may occur in corresponding parts of some other reefs, such as Yonge Reef, so making Cocos Atoll an imperfect basis for generalization.

(2) A failure to discriminate between those variations which are of specific value and those which are connected with environment.

If these two conditions had been altered, there would probably have been very little to choose between our views.

The conclusion, then, of both Dr. Fraser* and myself is this : That species undoubtedly exist among corals ; that they exist in considerable number ; that the growth forms and variations of detail to be found in any one species may also be considerable, but that after sufficient experience in the field, it is possible for a worker with a trained eye to determine in a great many cases which of the variations are specific and which are not ; that of the non-specific variations some are due to environmental causes, but that the effects of environment may easily be overstressed ; and that some of the variations are due to causes as yet unknown.

This does not mean that even the most experienced worker could identify every colony met with on a reef. There would be many which would defeat him, because the limits of variation are not by any means fully known as yet. But he would be able to distinguish *Acropora squamosa*, for instance, from any other species in a high proportion of cases. We feel there is very little doubt that the corals referred to in this paper by specific names do in fact represent entities of some definite description, for which the term "species" in its ordinarily accepted sense† is the most convenient term. Even if we suppose, for the sake of argument, that under some of our specific names we have in reality grouped a number of "micro-species" ; that here and there we have referred a colony to the wrong species altogether ; or that we have used for some of our species names to which they are not entitled ; still, these errors would not affect the main issue in the least (and needless to say every effort has been made to avoid them).

In choosing the photographs reproduced in the plates belonging to this paper, one of our aims was to illustrate some of the changes in form which may take place during the life-history of a single colony. Information of this description should prove useful to anyone whose task it is to attempt the identification of corals, since one of the difficulties which besets him is that of knowing what kind of allowance to make for the age of any colony which he may be studying. A study of the plates and their descriptions will show how, even among the small selection illustrated, the branches of some of the species maintain a fairly constant appearance though the form of the colony may change ; whereas in other cases the appearance of the branches alters quite definitely with increasing age.

Lastly, there is a factor in the situation which cannot be discussed fully here, since the evidence is not yet ready for publication ; but it will be shown in later reports in this volume, by S. M. Manton and by the present author, that certain coral species arrange themselves in the manner of so many other marine organisms, according to a distinct vertical zonation, on the reef. This factor possibly introduces a still further complication

* Dr. Fraser has, of course, read the manuscript of this paper.

† I cannot use space here to describe the sense in which I am using the word "species," but have attempted to explain this in another paper (1929, p. 163).

into Wood-Jones's arguments, because unless it were appreciated during a period of work on any reef, its effects might lend apparent but ephemeral support to arguments dealing with the general effects of environment.

SUMMARY AND CONCLUSIONS.

(1) The experiments described in this report dealt with the activities of 246 corals. They were carried out at Low Isles, Queensland, between July, 1928, and June, 1929. Four different experiments concerned with growth or regeneration were undertaken.

(2) The first experiment dealt with 169 corals, which were attached to concrete blocks and planted out on the reef in pools situated within 100 yards of the habitats from which they had been collected. These corals were all kept in two fenced-in pools, one in the anchorage and the other in the Western moat, the former representing an environment very favourable for coral growth, the latter a habitat subject to greater extremes of climate and suitable for the growth of a few species only. The growth of these corals is recorded during a period somewhat exceeding six months. It was found that the branching forms (*Psammocora*, *Pocillopora*, *Acropora* and *Montipora*) added, on an average, from 33 to 95% to their original diameter during this period: the average increase for these genera being summarized in the table on p. 179. It was also found that the average increase for massive corals belonging to the *Astracidae* (*Favia*, *Coeloria*, *Lobophyllia*, *Symphyllia*, *Galaxea*) was much smaller than that of the branched forms (10%), but that the average for massive forms of *Porites* was greater than that for the *Astracids* (17%). The various data obtained from this experiment are described on pp. 174–183.

(3) The second experiment dealt with 11 colonies only. Each of these was divided into halves: one half was kept in the moat and the other in the anchorage, both halves being attached to concrete blocks as in the first experiment. The results of this procedure are described on pp. 183–5, and it is concluded that in all probability those species which are normally inhabitants of the moat will grow well both there and in the anchorage, but that the species which normally inhabit the anchorage either will die under the more stringent conditions of the moat, will grow there less well, or will fail to attain normal size.

(4) The third experiment dealt with 30 colonies, which were marked *in situ* by a diver working below the level of low water, near the mouth of the anchorage. Details are recorded (pp. 185–8) referring to 11 of these colonies which were recovered after the experiment, and in which branches had been broken off, so that data concerning regeneration might be obtained: 144 regenerated branches were available for observation. The details of regeneration in *Acropora* are described, and it is shown that at least in the case of colonies of the irregular stagshorn type of growth, the amount of regeneration which takes place in individual healthy branches within a given period may be so different, that the new growth on one branch may be nearly ten times as great as that of another branch belonging to the same colony.

(5) In the fourth experiment (pp. 188–190) a variety of clean materials were fixed at various points on the reef, in the hope that coral planulae would settle upon them. About 40 young colonies established themselves on these materials, and 36 of these were recovered for measurement. The majority belonged to the species *Pocillopora bulbosa*, and it is shown that this species may form a flat expansion with diameters such as 11.0 ×

10.0 or 14.5×9.5 mm. in less than eleven months; and that during this time the first branch may arise on the expansion, attaining a height of 7 mm. and becoming trifid at the tip. Of the remaining colonies 7 belonged to the genus *Porites*, and the largest of these had formed expansions measuring 7.0×6.0 and 12.0×6.5 mm. in twenty-seven weeks.

(6) A number of the factors which influence the growth of corals are discussed (pp. 174-8) in connection with the results of the principal experiment. The conclusions may be summarized as follows:

(i) It has been shown clearly by Wood-Jones, Mayor and Edmondson that corals do not grow at an even rate, but by fits and starts, periods of growth alternating irregularly with periods in which there is little or no growth. The effects of this factor can be detected in the present experiments also, but it is possible nevertheless to distinguish more or less clearly between the effects of this and of other factors. This irregularity is best counteracted in experiments by continuing them for as long as possible; but the exact length of the experiment (within a few weeks) is of little significance, so long as it is not too short.

(ii) A coral may grow more actively in the anchorage (a favourable environment) than in the moat (a less favourable one); but the incidence of this factor varies very much according to species, and has apparently little effect in the case of corals whose normal habitat is the moat.

(iii) Small colonies of a species tend to grow more rapidly than larger colonies of the same species (this is confirmed by Mayor and Vaughan); but, except in the sense that when a colony has reached its maximum size it will grow no more, this rule does not apply rigidly and exceptions to it occur.

(iv) Individual variation appears to be a factor of importance. Corals belonging to the same species, and growing in the same environment for the same length of time, may grow at very different rates (irrespective of the size-factor); but the effects of individual variation and of irregularity of growth-rate are not easily disentangled.

(v) The form and internal structure of a colony should clearly affect the rate of growth, in the general sense that a branched species should grow more rapidly than a massive one, and one with light and slender branches more rapidly than one with stout, compact branches. This general tendency is confirmed by the results but has its exceptions.

(7) In the corals measured for the principal experiment, it was noticed (p. 181) that the average percentage increase in diameter for each of the principal genera was always higher in the case of the lesser of the two diameters measured than in the case of the greater. It is suggested that this may be due to a tendency on the part of the corals, when they can grow freely in all directions, to cover a more or less circular area, the coral growing more rapidly where it is narrower until this is attained. Certain data obtained from regenerating corals (p. 188) also suggest that if the symmetry of a colony is interrupted by damage (in a branching form), the branches which are regenerated, or which grow out from neighbouring branches, to fill the gap, grow rapidly until symmetry is restored.

(8) Some of the colonies of *Favia* and *Lobophyllia* used in the first experiment provided details of the asexual reproduction which had taken place in them during the experiment

(pp. 190–199). In the case of 6 colonies of *Favia*, the progress of 259 polyps was followed, and it was found that after about 8 months 158 of these had remained undivided, 77 had divided into two, 18 into three, and 6 into more than three new polyps, the total number at the end of the experiment being 394. In the case of 6 colonies of *Lobophyllia*, in which the polyps are much larger than in *Favia* and are meandrine in shape, there were 12 polyps to begin with, and these had increased to 16 at the end. The 12 original polyps had 47 mouths between them, but this number had increased to 59 after about 7 months. It is concluded that the reproduction in both genera was the result of intra-tentacular budding (at least in the majority of polyps), that no fission was involved, and that the new mouths were formed *de novo* and not split off from old ones.

(9) An account is given (pp. 201–3) of the distribution of the growth-forms of corals on one of the reefs of the Outer Barrier. It is maintained that this distribution calls for some modification in certain ideas which are prevalent concerning the relation between environment and growth-form in corals. Coupled with this is a discussion of the well-known views of Prof. F. Wood-Jones on the subject of species and forms of growth in corals; the conclusion is reached that species in the ordinarily accepted sense of the term do exist in many coral genera in considerable number, and that many of them may be fairly easily recognized in the field; and that Wood-Jones has considerably overstressed the effect of environmental conditions on the corals, although such an effect certainly exists, and is responsible for a considerable range of variation.

TABLES OF MEASUREMENTS.

EXPERIMENT I.

In the following table, under each species or variety, corals kept in the anchorage pen are listed first, those kept in the moat pen afterwards; corals of the same species, kept in the same pen, are listed in order of size, starting with the smallest, and taking the initial greater diameter as the index-figure. The numbers in column 1 of the table are numbers which were engraved on the cement blocks; therefore if a coral is numbered 62*a*, this indicates that it was attached to block 62, but that this block had more than one coral fastened to it, the colonies being distinguished as 62*a*, 62*b*, etc. In cases where no "remarks" occur in the last column, it may be assumed that the growth of the coral was normal. Percentages are expressed to the nearest whole number, except in the case of those below 1%.

EXPERIMENT II.

In this experiment a number of colonies were divided into halves. The system of reference numbers adopted for the halves was as follows: The letter A denotes a half-colony whose complementary half bears the symbol B. Thus, when a given colony was divided, one half was called A1, the other B1; in the case of a second colony, one half was A2, the other half B2; and so on. In the table, the series of measurements applying to the two halves of any one colony are included immediately following one another, so that the results for the two halves may readily be compared.

EXPERIMENT I.

A = anchorage; M = moat. Measurements in centimetres. See also note on p. 209.

Reference No.	Genus.	Species.	Place of origin.	Pen in which kept.	Period of growth.		Initial greater diameter.	Increase on greater diameter.		Initial lesser diameter.	Increase on lesser diameter.		Remarks.
					Weeks.	Days.		Actual increase.	Percentage increase.		Actual increase.	Percentage increase.	
62a	<i>Lecanora</i>	<i>squamosa</i>	A	A	29	2	9.07	9.60	106	8.20	8.61	105	
61a	"	"	A	A	29	2	10.72	3.10	29	10.11	5.41	54	
40a	"	"	A	A	29	6	14.35	4.14	29	13.36	3.50	26	
7	"	"	A	A	30	1	21.13	7.37	35	16.21	6.40	39	
1	"	"	A	A	30	1	21.34	7.62	36	16.26	6.91	42	
57	"	"	A	A	29	2	24.00	8.26	34	21.46	7.24	34	
59	"	"	A	A	29	2	24.08	9.02	37	21.08	6.55	31	
35b	"	"	M	M	34	5	4.29	6.45	150	4.17	7.70	185	
64b	"	"	M	M	33	3	6.59	5.11	78	3.40	5.53	34	
63a	"	"	M	M	23	4	7.49	0.91	12	4.62	1.55	34	Died before end of experiment.
17b	"	"	M	M	34	6	12.22	3.53	29	8.03	1.80	22	Growth subnormal. Dead by end of experiment.
19	"	"	M	M	35	1	13.72	0.84	6	7.01	2.64	38	
35a	"	"	M	M	34	5	15.01	2.62	17	10.54	2.46	23	
62b	"	<i>quelchi</i>	A	A	29	2	8.08	7.19	89	7.75	6.78	87	
60a	"	"	A	A	26	5	10.85	6.15	57	10.13	7.90	78	
40b	"	"	A	A	29	6	11.20	4.88	44	9.96	3.36	34	
4	"	"	A	A	30	1	15.16	7.01	46	11.86	6.78	57	
56	"	"	A	A	29	5	16.18	6.43	40	15.19	4.47	29	
68c	"	<i>quelchi</i> , var. 1	M	M	33	4	4.37	2.24	51	2.61	2.01	77	
63b	"	"	M	M	32	2	5.16	3.07	59	4.24	2.74	65	
68a	"	"	M	M	22	1	5.61	2.08	37	5.16	1.37	27	
68b	"	"	M	M	33	4	5.87	2.54	43	3.71	3.53	95	Died before end of experiment.
67b	"	"	M	M	22	1	6.20	1.40	23	5.94	0.97	16	
64a	"	"	M	M	22	0	8.95	3.78	42	8.28	3.48	42	Died before end of experiment.
65a	"	"	M	M	33	4	9.55	4.57	48	6.07	2.79	46	"
65b	"	"	M	M	33	4	9.80	4.32	44	9.17	5.87	64	"
55a	"	<i>quelchi</i> , var. 2	A	A	28	0	8.51	2.69	32	7.85	4.51	57	
58	"	"	A	A	29	5	12.37	8.10	65	11.79	8.23	70	
38a	"	<i>pulchra</i>	A	A	27	6	8.99	7.44	83	8.99	9.68	108	
37	"	"	A	A	29	6	15.72	11.33	72	14.61	11.81	81	
51	"	"	A	A	29	5	15.98	11.40	71	14.94	10.34	69	
3	"	"	A	A	30	1	28.07	3.61	13	25.88	8.58	33	
95	"	<i>exilis</i>	A	A	27	6	18.10	9.09	50	16.56	9.47	57	
5	"	"	A	A	30	1	23.85	8.66	36	14.55	3.33	23	
97	"	<i>formosa</i>	A	A	27	6	22.02	8.46	38	18.59	8.69	47	
43b	"	<i>gemmifera</i>	A	A	28	0	11.05	4.29	39	8.53	4.90	57	
6	"	"	A	A	30	1	13.97	3.20	23	13.84	1.80	13	
60b	"	<i>hyacinthus</i>	A	A	26	5	7.06	6.99	99	6.22	7.90	127	
55b	"	Not determined	A	A	28	0	3.66	2.44	67	2.54	4.01	158	
67a	"	"	M	M	22	1	5.16	1.37	27	3.58	3.12	87	Died before end of experiment.
66b	"	"	M	M	33	4	5.84	1.27	22	5.38	3.96	74	
66a	"	"	M	M	22	1	6.38	2.21	35	3.43	1.07	31	
63c	"	"	M	M	32	2	6.45	2.92	45	5.99	1.66	23	
8	"	"	A	A	26	6	18.21	0.02	0.1	17.42	0.76	4	
44	"	<i>ramosa</i>	A	A	29	6	15.32	6.43	42	11.73	6.15	52	
81a	"	"	M	M	31	2	1.83	2.49	136	1.42	3.23	227	

EXPERIMENT I—continued.

A = anchorage; M = moat. Measurements in centimetres. See also note on p. 209.

Reference No.	Genus.	Species.	Place of origin.	Pen in which kept.	Period of growth.		Initial greater diameter.	Increase on greater diameter.		Initial lesser diameter.	Increase on lesser diameter.		Remarks.
					Weeks.	Days.		Actual increase.	Percentage increase.		Actual increase.	Percentage increase.	
54b	<i>Lobophyllia</i>	Species 2	A	A	29	5	7.37	0.79	11	6.86	0.99	14	Part of this specimen died.
85	"	"	M	M	32	5	21.59	0.79	4	21.16	No second measurement	6	
86	"	"	M	M	32	5	21.89	0.25	1	12.24	0.76	6	Nos. 85 and 86 were halves of a single large colony.
45b	"	Species 3	A	A	29	1	7.06	0.25	4	6.68	0.38	6	
45a	"	Species 4	A	A	29	1	10.29	0.05	0.5	4.57	0.46	10	Not a very healthy specimen.
46	"	"	A	A	27	6	10.85	0	0	4.70	0.08	2	
92c	"	Not determined	Batt Reef	A	26	5	4.98	1.02	20	4.60	1.04	23	Died before end of experiment.
53a	"	"	A	A	29	5	5.54	0.97	18	5.08	0.79	16	
53b	"	"	A	A	29	5	5.87	0.89	15	4.09	0.56	14	Died before end of experiment.
92b	<i>Symphyllia</i>	" recta	M	M	26	5	3.40	0.64	19	3.02	0.89	29	
36a	"	"	M	M	34	5	5.49	0.61	11	4.95	0.86	17	Died before end of experiment.
77a	"	"	M	M	33	0	9.22	0.86	9	8.64	0.86	10	
91	"	"	M	M	32	5	11.66	0.15	1	10.46	0.18	2	Unhealthy at first, but recovered fully later.
88	"	"	M	M	32	5	16.02	0.56	3	15.39	0.76	5	
11	"	"	M	M	32	3	20.73	1.07	5	17.75	0.76	4	Unhealthy at first; flourished very well later.
16b	<i>Fungia</i>	" fungites	M	M	23	4	6.55	0.67	10	5.64	0.74	13	
15a	"	"	M	M	35	1	7.75	0.86	11	6.63	0.69	10	Unhealthy at first, but recovered fully later.
15b	"	"	M	M	23	5	8.08	0.28	3	7.87	0.02	0.3	
84b	"	"	M	M	19	6	9.78	0.41	4	9.73	0.28	3	Unhealthy at first; flourished very well later.
16a	"	"	M	M	35	0	11.07	0.38	3	10.86	0	0	
47a	"	" fungites, var. 1	M	A	26	5	12.07	0.02	0.2	10.49	0.23	2	Nos. 73 and 82 were portions of a single large colony.
98	"	"	A	A	27	6	17.55	0.08	0.4	18.47	0	0	
47b	"	<i>actiniformis</i> var. <i>crassitentaculata</i>	A	A	26	5	11.40	0.30	3	9.42	0.61	6	Probably died soon after beginning of experiment.
32	<i>Döderleinia</i>	" <i>irregularis</i>	A	A	28	0	34.34	0.66	2	24.41	0.71	3	
100	"	Species 1	A	A	26	5	26.11	0.58	2	11.84	0	0	Probably died soon after beginning of experiment.
33b	<i>Herpæditha</i>	" <i>gonagra</i>	M	M	35	0	5.84	3.30	57	5.56	2.71	49	
89c	<i>Psammocora</i>	"	M	M	32	5	7.19	2.57	36	5.41	2.84	52	Probably died soon after beginning of experiment.
89b	"	"	M	M	32	5	7.44	3.15	42	7.32	2.90	40	
33a	"	"	M	M	35	0	7.80	2.64	34	6.02	2.90	48	Probably died soon after beginning of experiment.
75b	"	"	M	M	31	2	8.41	2.87	34	7.62	2.69	35	
84a	"	"	M	M	31	2	11.68	2.77	24	9.73	3.81	39	Probably died soon after beginning of experiment.
75a	"	"	M	M	31	2	13.69	2.95	22	10.82	2.69	25	
90	"	"	M	M	32	5	17.22	3.10	18	15.19	2.77	18	Probably died soon after beginning of experiment.
89a	"	"	M	M	32	5	17.68	2.69	15	15.75	2.13	14	
73	<i>Pavona</i>	" cactus	M	M	33	1	15.24	3.81	25	14.68	2.16	15	Probably died soon after beginning of experiment.
82	"	"	M	M	32	5	22.28	2.46	11	18.59	2.34	13	
24b	<i>Lobophyllum</i>	near <i>crebriripicatum</i>	M	M	35	0	12.09	7.67	63	9.12	6.58	72	Probably died soon after beginning of experiment.
43a	"	Species 1	A	A	28	0	7.82	1.55	20	7.62	1.96	26	
61b	<i>Sinularia</i>	"	A	A	29	2	5.66	3.20	57	5.21	2.24	43	Probably died soon after beginning of experiment.
99	<i>Heliopora</i>	" <i>coerulea</i>	A	A	26	6	28.83	0.82	3	26.57	0.91	3	

EXPERIMENT II.

A = anchorage; M = moat. Measurements in centimetres. See also note on p. 209.

Reference No.	Genus.	Species.	Place of origin.	Pen of which kept.	Period of growth.		Initial greater diameter.	Increase on greater diameter.		Initial lesser diameter.	Increase on lesser diameter.		Remarks.
					Weeks.	Days.		Actual increase.	Percentage increase.		Actual increase.	Percentage increase.	
A2	<i>Acropora</i>	<i>squamosa</i>	M	A	27	0	7.19	3.68	51	6.86	5.18	76	Growth probably subnormal. Made no progress. Died a few days after transplantation.
B2	"	"	M	M	31	3	7.29	1.37	19	6.83	1.50	22	
A1	"	<i>quelchi</i> , var. 1	M	A	27	0	4.90	1.73	35	4.04	2.18	54	
B1	"	"	M	M									
A10	"	<i>exilis</i>	A	A	26	5	15.39	6.15	40	13.00	6.10	47	
B10	"	"	A	M									Much broken; smaller at end of experiment than at beginning. Died slowly. Discarded 20 weeks after beginning of experiment. Died a few days after transplantation.
A9	"	<i>formosa</i>	A	A	26	5	14.68	10.52	72	14.30	10.39	73	
B9	"	"	A	M	Was dead all but one twig 10 weeks after beginning of experiment; but ultimately died also.								
A8	"	<i>hebes</i>	M	A									
B8	"	"	M	M	31	3	14.17	8.42	59	16.33	7.42	45	
A3	"	"	M	A	27	0	12.75	5.16	40	11.35	5.76	51	Died slowly. Discarded 20 weeks after beginning of experiment. Died a few days after transplantation.
B3	"	"	M	M									
A7	"	Species 1	M	A	27	1	10.62	4.39	41	8.74	7.09	81	
B7	"	"	M	M	31	3	9.98	5.26	53	5.11	1.09	21	
A5	<i>Montipora</i>	<i>ramosa</i>	M	M	31	1	13.06	3.28	25	9.02	1.70	19	
B5	"	"	M	A	27	1	12.98	7.98	61	9.56	6.35	66	Died a few days after transplantation.
A11	"	foliose form	M	A									
B11	"	"	A	A	26	5	23.22	4.67	20	20.68	5.77	28	
A4	<i>Pocillopora</i>	<i>bulbosa</i>	M	M	31	1	7.90	0.99	13	3.91	3.15	81	
B4	"	"	M	A	27	1	7.58	3.05	40	6.63	2.51	38	
A6	"	"	M	M	31	1	15.29	3.45	23	14.40	3.84	27	Died a few days after transplantation.
B6	"	"	M	A	27	1	12.45	4.06	33	11.99	4.14	35	

EXPERIMENT III.

In this experiment branches were broken from a number of colonies, which were marked in the manner described on p. 173. The colonies were left growing *in situ*, the work being carried out by a diver. All the colonies were situated near the mouth of the anchorage.

Reference No.	Genus.	Species.	Period of experiment.		Method of marking.	Number of regenerating branches which had subdivided.	Lengths of regenerated portions of individual branches in millimetres. Measured from the point of fracture to the tip of the new branch. Where two or more branches were the same length, the number of these is given in brackets after the length concerned.
			Weeks.	Days.			
1	<i>Acropora</i>	<i>formosa</i>	14	0	Branches marked separately	3	3.0, 3.25, 6.0, 6.5, 7.75, 8.0 (2), 8.75, 9.5, 10.0, 10.5, 14.25, 14.5 (2), 18.5, 19.5, 21.5 (2), 23.75.
2	"	"	7	1	Ditto	0	1.5, 2.0, 3.5 (3), 5.5.
3	"	"	15	3	"	0	<1.0 (2), 1.25, 3.0, 5.0, 8.0, 8.5.
4	"	<i>gemmifera</i>	15	2	Group of branches marked	0	6.0, 6.5, 7.5 (2), 8.25, 8.75, 9.5, 10.0, 11.0, 12.0 (2). The new branches had not in the main attained the same level as the old ones. Only a proportion of the new ones could be measured, since in the rest the point of breakage could not be identified.
5	"	"	13	5	Ditto	0	3.5, 6.0, 6.5, 7.0, 7.25 (2), 7.5 (3), 7.75, 8.0, 8.25, 8.5, 9.25 (3). The new branches had not in the main attained the same level as the old ones. Most of the new branches were measurable, since the breakage point was easily identified.
6	"	<i>quelchi</i>	15	2	"	0	2.0, 4.5, 4.75, 6.75, 9.0, 10.5, 11.0, 11.5, 12.75. The same remark applies as in No. 4.
7	"	"	13	5	Branches marked separately	0	<1.0 (2), 2.5, 2.75, 3.5, 4.0, 4.25, 4.5 (3), 5.25, 5.5, 6.5, 7.0 (2), 9.25.
8	"	<i>polymorpha</i>	13	5	Ditto	6	14.25, 15.0, 17.25, 21.25, 22.75, 25.5.
9	"	"	25	3	"	2	4.0, 6.0, 9.0, 11.0, 12.0, 17.0, 17.25, 19.25, 21.0, 29.0, 33.5, 35.0, 38.75.
10	"	Species 2	13	5	"	1	5.0, 5.5, 6.0, 6.5, 7.5 (2), 8.0, 8.5 (2), 8.75, 9.0 (3), 9.5, 10.0, 10.25, 10.5 (3), 11.75, 13.5, 13.75.
11	"	" 3	13	5	"	0	<1.0 (9), 1.5, 2.0 (3), 2.75, 3.5, 5.0, 6.0, 7.5.

EXPERIMENT IV.

In this experiment coral planulae were allowed to settle upon clean materials which had been planted out on the reef. The dimensions of colonies which developed from such planulae are recorded, and measurements of certain other organisms which also settled on the materials provided are added. Most of the colonies were still in the form of flattened expansions, in which case two diameters are given, taken more or less at right angles to one another. In other cases a vertical branch had arisen; for these the height of the branch is also recorded.

EXPERIMENT IV.

See note on p. 214.

Reference No.	Name of organism.	Locality in which the larvae settled.	Period of experiment.		Diameters in millimetres.	Height of branch, when present, in millimetres.	Reference No.	Name of organism.	Locality in which the larvae settled.	Period of experiment.		Diameters in millimetres.	Height of branch, when present, in millimetres.
			Weeks.	Days.						Weeks.	Days.		
1	<i>Pocillopora bulbosa</i>	Madrepore moat	42	5	1.3	1.1	34	<i>Cyphastrea</i> sp.	Porites pond	42	5	7.4	6.5
2	"	"	42	5	2.8	2.5	35	Undetermined coral	Western moat	43	0	4.7	4.4
3	"	"	42	5	3.3	3.2	36	Ditto	Porites pond	42	5	4.0	3.3
4	"	"	42	5	3.7	2.9	37	"	Madrepore moat	14	0	10.0	8.2
5	"	"	42	5	4.5	3.0	38	"	"	14	0	17.0	15.3
6	"	"	42	5	4.5	3.5	39	<i>Anomia ? cytaeum</i>	Porites pond	42	5	9.8	7.8
7	"	"	42	5	5.5	5.0	40	"	Anchorage	36	2	14.9	14.8
8	"	"	42	5	5.5	5.0	41	<i>Pinctada panasesae</i>	"	43	0	17.9	13.4
9	"	"	42	5	6.5	5.0	42	"	Porites pond	42	5	11.0	9.2
10	"	"	42	5	7.0	5.5	43	<i>Spondylus hystrix</i>	"	42	5	12.5	11.4
11	"	"	42	5	7.5	5.5	44	"	"	42	5	13.5	11.3
12	"	"	42	5	8.0	7.5	45	"	Anchorage	43	0	17.0	16.9
13	"	"	42	5	8.5	6.9	46	<i>Spondylus ? hystrix</i>	"	42	5	25.4	24.8
14	"	"	42	5	9.0	6.5	47	<i>Ostrea cerata</i>	Porites pond	42	5	25.8	18.5
15	"	"	42	5	9.0	8.0	48	"	"	42	5	9.4	5.1
16	"	"	42	5	11.0	10.0	49	<i>Barbatia decussata</i>	"	42	5	10.0	
17	"	Western moat	43	3	1.7	1.6	50	<i>Vermetus</i> sp.	"	42	5	12.8	
18	"	"	43	0	2.6	2.3	51	"	"	42	5	11.9	
19	"	"	43	0	3.5	3.4	52	"	Anchorage	43	0	51.15 (length)	
20	"	"	43	0	7.5	6.0	53	"	"	36	2	62.5	13.0
21	"	Porites pond	42	5	2.7	2.6	54	Polychaet tube	"	36	2	Length of individual branches	
22	"	"	42	5	4.5	4.0	55	"	"	36	2	65.0 (3), 75.0	
23	"	"	42	5	5.7	4.9	56	Sponge	"	36	2	80.0, 95.0,	
24	"	"	42	5	10.4	7.7		<i>Gellius fibulatus</i>	Western moat	16		100.0, 105.0	
25	"	"	42	5	14.5	9.5						12.0 wide;	
26	"	Mouth of anchorage	12	3	1.8	1.7						21.0 high	
27	<i>Porites</i> sp.	Western moat	27	1	7.0	6.0						19.2 wide;	
28	"	"	27	1	12.0	6.5						13.0 high	
29	"	Porites pond	27	1	3.6	3.1	57	<i>Retepora graeffei</i>	Anchorage	43	0		
30	"	"	42	5	3.6	3.1	58	"	"	43	0		
31	"	"	42	5	3.7	3.6							
32	"	"	42	5	5.4	3.9							
33	"	"	42	5	6.6	5.9							

REFERENCES.

From the following works further references to investigations on growth and asexual reproduction in corals may be obtained :

- CROSSLAND, C. 1931. The Reduced Building-power and Other Variation in the Astrean corals of Tahiti, with a Note on *Herpetolitha limax* and *Fungia* spp. Proc. Zool. Soc. Lond. pp. 351-92, pls. 1-22, text illust.
- DUERDEN, J. E. 1902. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci. Washington, VIII, pp. 397-599, pls. 1-25, text illust.
- EDMONDSON, C. H. 1929. Growth of Hawaiian Corals. Bull. Bishop Mus. Honolulu, LVIII, pp. 38, 5 pls., text illust.
- GARDINER, J. S. 1901-6. The Fauna and Geography of the Maldive and Laccadive Archipelagoes. 2 vols., 100 pls., text illust. Cambridge.
- MARSHALL, S. M., and ORR, A. P. 1931. Sedimentation on Low Isles Reef and its Relation to Coral Growth. Sci. Rep. Gt. Barrier Reef Exped. 1928-29, I, pp. 93-133, pls. 1-3, text-illust.
- MATTHAI, G. 1926. Colony-formation in Astraeid Corals. Philos. Trans. London, Ser. B, CCXIV, pp. 313-367, pls. 24-28, text-illust.
- MAYOR, A. G. 1924. Growth-rate of Samoan Corals. Pap. Dept. Mar. Biol. Carn. Instn. Wash. XIX, pp. 51-72, pls. 1-26.
- STEPHENSON, T. A. 1929. On Methods of Reproduction as Specific Characters. J. Mar. Biol. Ass. Plymouth, XVI, pp. 131-172, text illust.
- and A., TANDY, G., and SPENDER, M. A. 1931. The Structure and Ecology of Low Isles and Other Reefs. Sci. Rep. Gt. Barrier Reef Exped. 1928-29, III, pp. 17-112, pls. 1-27, text illust.
- 1931. Development and the Formation of Colonies in *Pocillopora* and *Porites*—Part I. Sci. Rep. Gt. Barrier Reef Exped. 1928-29, III, pp. 113-134, pls. 1-6, text illust.
- VAUGHAN, T. W. 1916. On Recent Madreporaria of Florida, the Bahamas, and the West Indies, and on Collections from Murray Island, Australia. Yearb. Carn. Instn. Wash. XIV, pp. 220-31.
- 1918. Some Shoal-water Corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island. Pap. Dept. Mar. Biol. Carn. Instn. Wash. IX, pp. 49-234, pls. 20-93, text illust.
- WOOD-JONES, F. 1907. On the Growth-forms and Supposed Species in Corals. Proc. Zool. Soc. Lond. pp. 518-556, pls. 27-29, text illust.
- 1912. Coral and Atolls, pp. xxiii + 392, 27 pls., text illust. London. (First issued 1910, reissued 1912.)

SYSTEMATIC INDEX

	PAGE		PAGE
Acropora	173, 179, 182, 189, 200, 207	Herpetolitha	181-2, 212
„ decipiens	201	Hormothamnium solutum	173
„ delicatula	201-4		
„ exilis	180, 183, 210, 213	Lobophyllia	179, 181-2, 194-9, 207-9
„ formosa	180, 183, 185, 188, 210, 213-14	„ corymbosa	211
„ gemmifera	180, 187, 188, 201-2, 210, 214	„ undetermined species	211-12
„ hebes	184, 201, 213	Lobophytum crebriplicatum	212
„ hyacinthus	180, 203, 210	„ undetermined species	212
„ palifera	180	Lyngbya majuscula	173
„ polymorpha	186-8, 214		
„ pulchra	180, 202, 210	Madrepora 203; see also Acropora.	
„ quelchi	177, 180, 184, 188, 210, 213-14	Microphytic algae	189
„ squamosa	175, 180, 184, 187, 201, 203, 206, 210, 213	Montipora	207
„ undetermined species	175, 184, 210, 213-14	„ foliose species	180, 183, 211, 213
Actinians	191	„ ramosa	178-80, 182-3, 210-11, 213
Alcyonaria	181	Ostrea cerata	215
Anomia cytaeum	215	Oysters	190, 215
Astraeidae	181, 207		
Barbatia decussata	215	Padina	189
Coeloria	181-2, 207	Pavona cactus	181, 212
„ daedalea	179, 211	Pinctada panasesae	215
Corynactis	191	Pocillopora	179, 182, 187, 190
Cyanophyceae	173	„ brevicornis	205
Cyphastrea	189, 215	„ bulbosa	176-7, 183, 188-9, 207, 211, 213, 215
		„ nobilis	205
Döderleinia	181	Polychaet tubes	215
„ irregularis	212	Porites	177, 179, 182, 189, 190, 207-8, 211, 215
		Psammocora	179, 181, 182, 207
Favia	179, 181-2, 191-5, 207-9	„ gonagra	212
„ doreyensis	194, 211		
„ favus	194, 211	Retepora graeffei	189, 215
„ halicora	211		
„ pectinata	211	Seriatopora	180
„ undetermined species	194, 211	„ hystrix	211
Fungia actiniformis	181, 212	Sinularia	212
„ fungites	181, 212	Spondylus hystrix	215
		Sponge	215
Galaxea	207	Symphyllia	179, 181, 182, 207
„ musicalis	181, 211	„ recta	212
Gellius fibulatus	190, 215		
Goniastrea pectinata	211	Turbinaria	210
„ undetermined species	211		
Helipora coerulea	181, 212	Undetermined coral	189, 215
		Vermetidae	190
		Vermetus	215

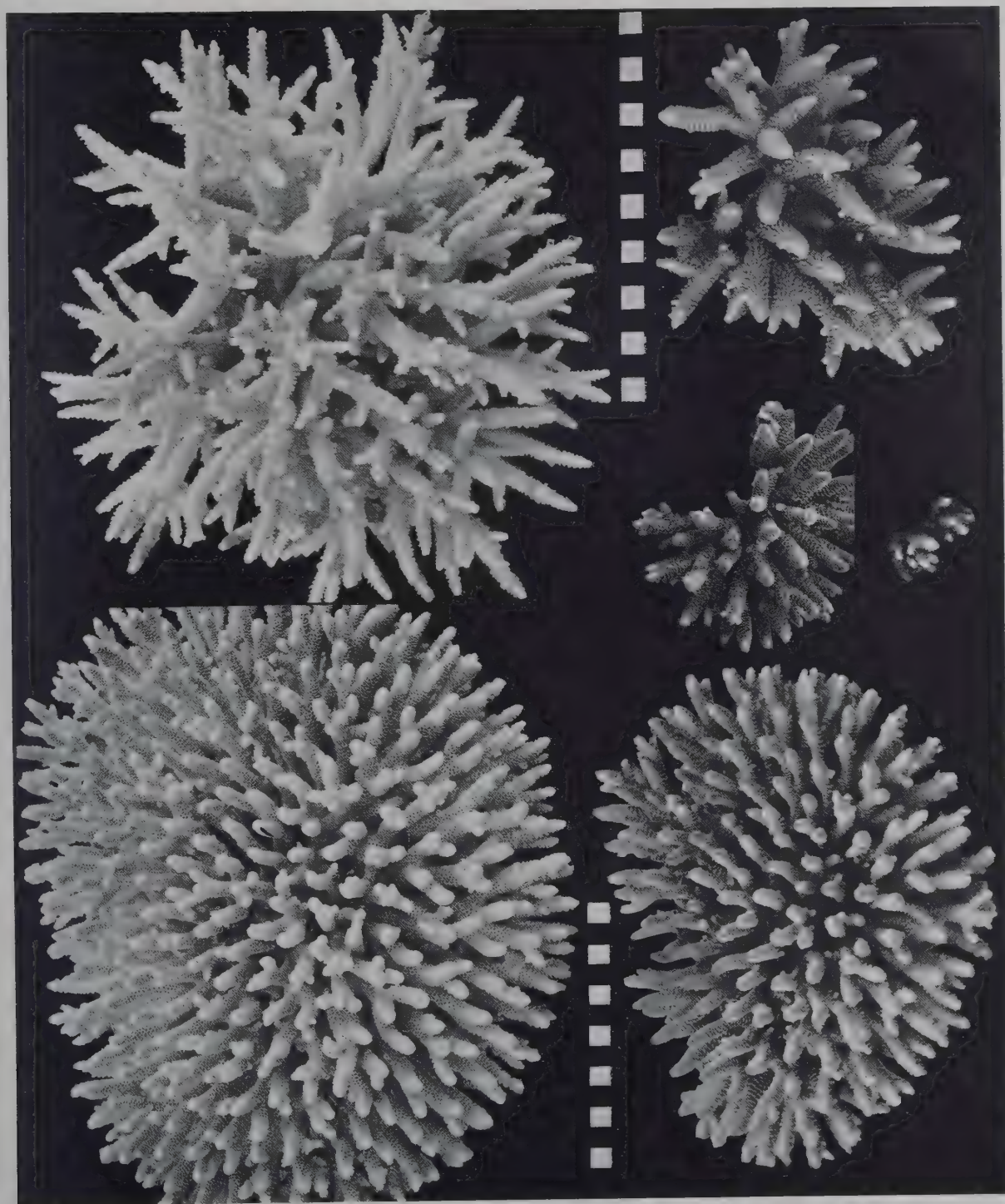
DESCRIPTION OF PLATE I.

(In this plate, and also in Plates II to VII, the scale is indicated wherever possible by rows of black and white squares, which represent square centimetres, and which were photographed at the same time as the corals; these squares are approximate, and do not represent the scale from which the actual measurements were made. Except in Plate VII, fig. 5, the row of squares is placed in all cases *between* the two photographs which represent the same coral at the beginning and end of the experiment; as a guide to the eye. In all cases where two photographs of the same coral are given, from the same point of view, they are to the same scale.)

GROWTH IN COLONIES OF ACROPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1 and 2.—*Acropora pulchra*. Experiment I, no. 37. Collected and planted out in the anchorage. This specimen showed an increase of 72% and 81% on its greater and lesser diameters respectively, during a period of 29 weeks and 6 days. The remarkable increase in the *area* covered by the coral, within the $7\frac{1}{2}$ months, is obvious from the photographs. The growth-form has not changed markedly.

FIGS. 3-6.—*Acropora squamosa*. Figs. 3 and 4, Experiment I, no. 35*b*, collected and planted out in the moat. Figs. 5 and 6, Experiment I, no. 57, collected and planted out in the anchorage. In figs. 3 and 4 an enormous relative increase in a very young colony is illustrated (150% and 185% on the greater and lesser diameters respectively); in figs. 5 and 6 the colony was much larger at the beginning of the experiment; the increase in size is still considerable (34% on each of the two diameters), but not as great as in the case of the small colony. The period of experiment for the small colony was 34 weeks and 5 days, for the larger one 29 weeks and 2 days. The scale of the small colony is not given on the plate; its initial greater diameter was 4.29 cm. A further example of growth in this species is given in Plate II, figs. 1 and 2.



DESCRIPTION OF PLATE II.

GROWTH IN COLONIES OF ACROPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1 and 2.—*Acropora squamosa*. Experiment I, no. 62a. Collected and planted out in the anchorage.

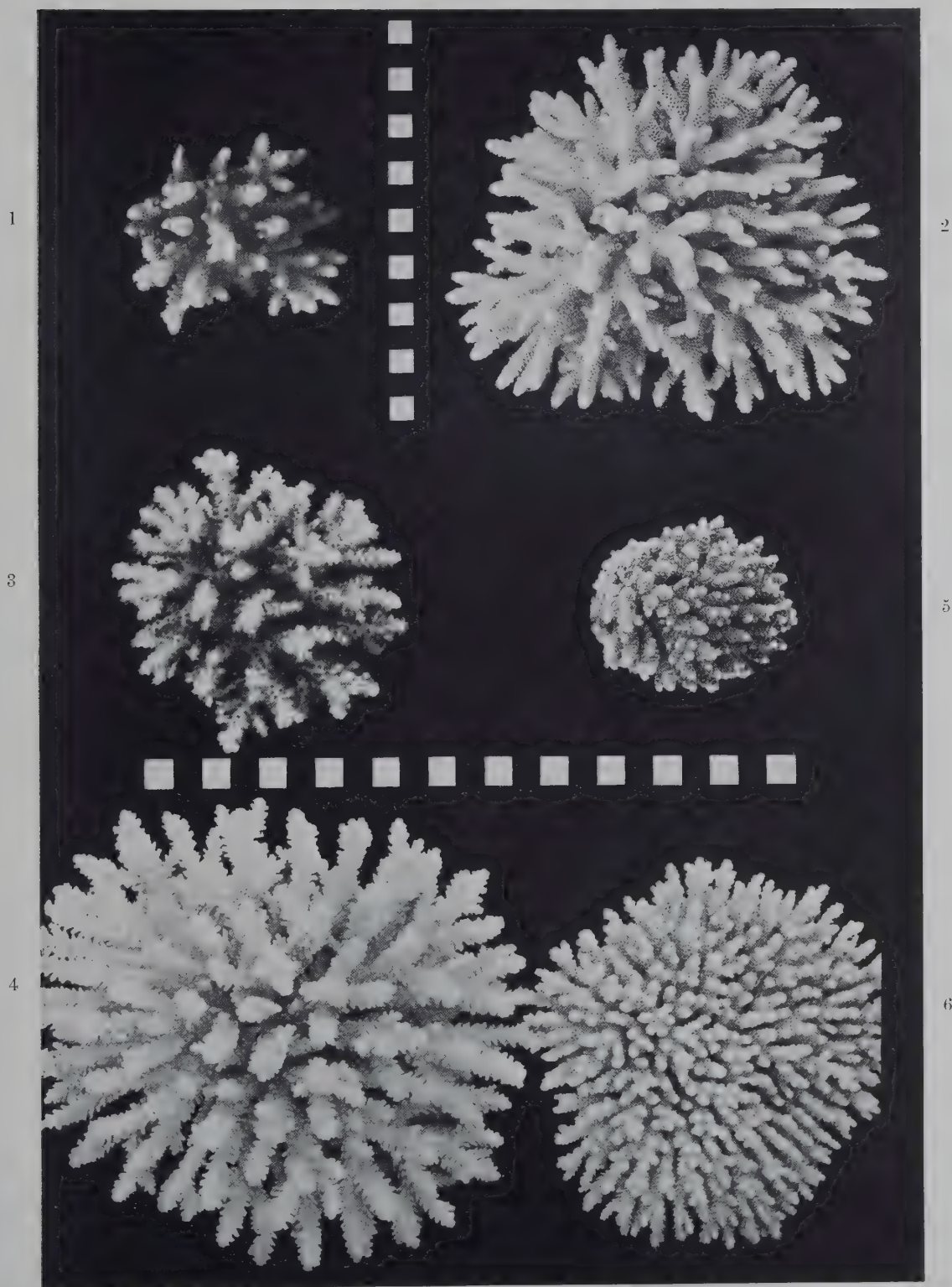
This specimen was intermediate in size between the two colonies of the same species illustrated in Plate I; and its growth was of intermediate amount (106% and 105% on the two diameters in 29 weeks and 2 days). The several photographs of this species illustrate the change from a somewhat irregular shape in the young colony, to the adult condition in which the colony forms a cyathiform or bracket-like expansion, flat on the top and with a stout stem below; but the appearance of the individual branches changes very little after the colony has attained a diameter of a few centimetres, making the species as a rule readily recognizable.

FIGS. 3 and 4.—*Acropora quelchi*. Experiment I, no. 60a. Collected and planted out in the anchorage.

Another species with branches of medium thickness in which growth is rapid. In this case the increase was 57% and 78% on the greater and lesser diameters respectively, in a period of 26 weeks and 5 days.

FIGS. 5 and 6.—*Acropora hyacinthus*. Experiment I, no. 60b. Collected and planted out in the anchorage.

This is one of the most delicately branched species of *Acropora* found at Low Isles, but is the one which grows to the largest size, frequently forming shelf-like brackets which project from the sides of rocky masses and are 6 or 8 ft. in diameter. The young colony forms a rounded bush (fig. 5); when older, if able to extend freely in all directions, it forms a vase-like structure (it has attained this stage in fig. 6, a side view of which is shown in Plate X, fig. 6); the growth subsequently tends to become less symmetrical, and the adult frequently forms a shelf attached at one side only. The increase of size in this specimen was 99% and 127% on the greater and lesser diameters in 26 weeks and 5 days.



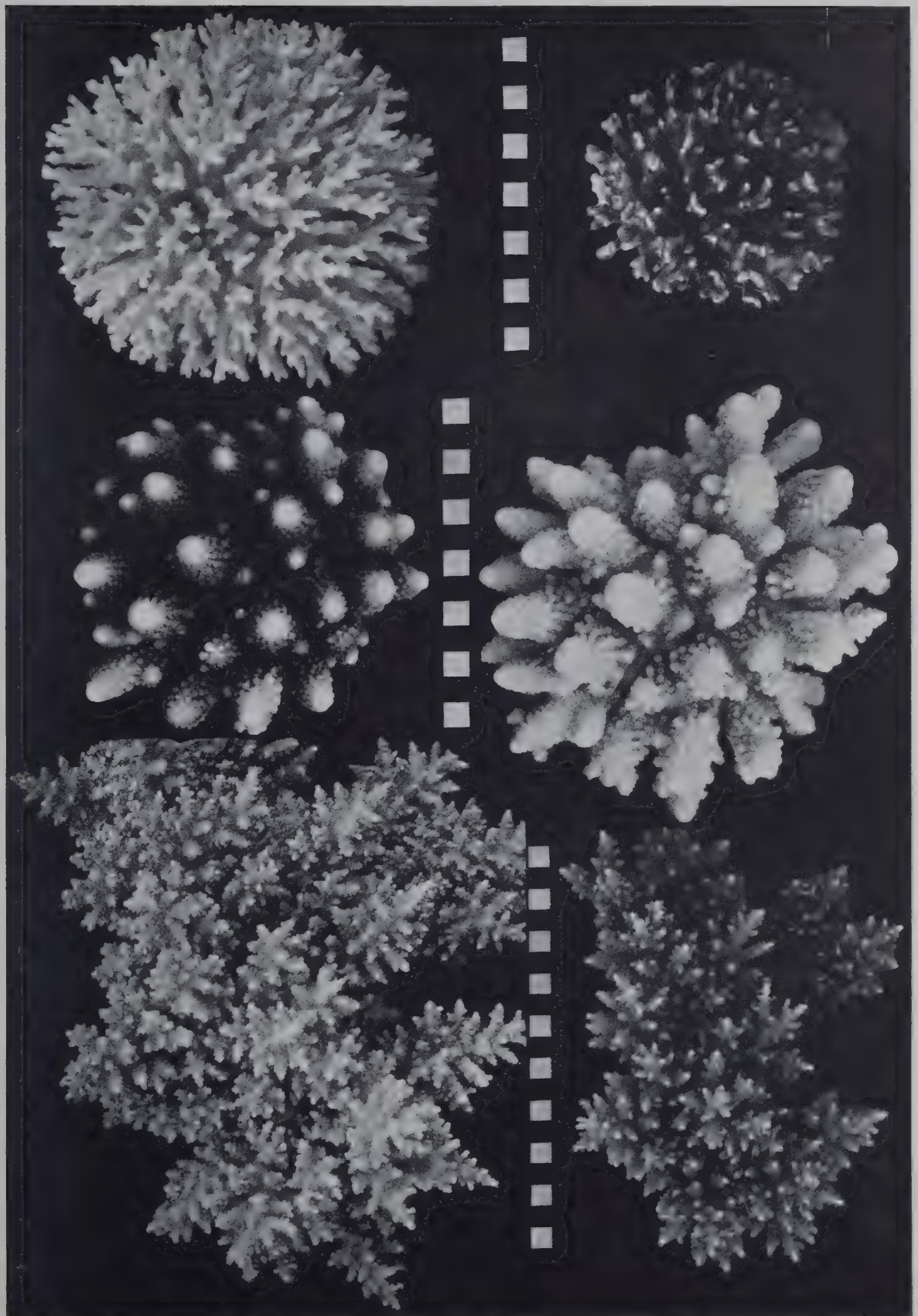
DESCRIPTION OF PLATE III.

GROWTH IN COLONIES OF ACROPORA AND POCILLOPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1 and 2.—*Pocillopora bulbosa*. Experiment I, no. 32. Collected and planted out in the moat. Increase 48% and 54% on the two diameters, in 35 weeks. The figures illustrate the amount of growth in a common moat-living species accustomed to high temperatures during the period of low water in the summer. The coral has maintained a similar aspect throughout the period of the experiment, which is in contrast to the change which has taken place in specimens of another common moat species in the same pool (Plate V, figs. 6 and 7).

FIGS. 3 and 4.—*Acropora gemmifera*. Experiment I, no. 6. Collected and planted out in the anchorage. Here the growth is considerably less than in the other species of *Acropora* illustrated, on account of the massive nature of the branches. The increase was 23% and 13% on the two diameters, in 30 weeks 1 day.

FIGS. 5 and 6.—*Acropora exilis*. Experiment I, no. 95. Collected and planted out in the anchorage. This species illustrates the extreme reached by the genus, at Low Isles, in the direction of a high degree of subdivision of delicate branches; and this form of growth is associated with fairly rapid increase in size (50% and 57% increase on two diameters, in 27 weeks 6 days).



DESCRIPTION OF PLATE IV.

GROWTH IN FOLIOSE SPECIES OF MONTIPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1 and 2.—A foliose species of *Montipora*. Experiment II, no. B 11. Collected and planted out in the anchorage. The growth has been considerable (20% and 28% increase on two diameters in 26 weeks 5 days), and the complexity of the folding has increased as growth proceeded.

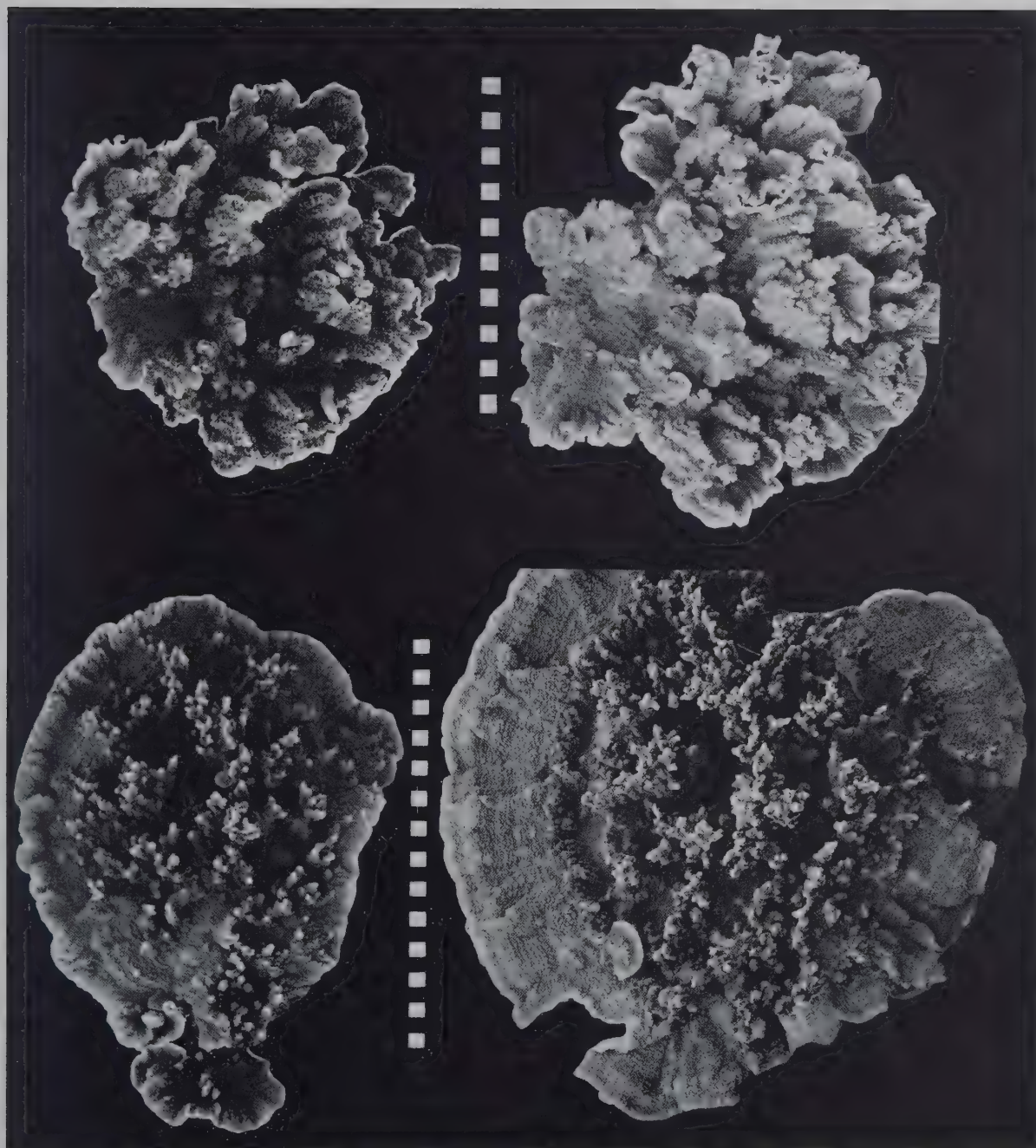
FIGS. 3 and 4.—A species of *Montipora* with upright branches in the centre and a foliose margin. Experiment I, no. 93. Collected and planted out in the anchorage. The marginal shelf has increased very much in width during the experiment; the branches have also grown upwards considerably, but foreshortening has masked this in the photograph. The increase in diameter was 21% and 54% on the greater and lesser diameters respectively, in 27 weeks 6 days.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).

REPORTS, VOL. III, No. 7.

PLATE IV.



Photographs by T. A. Stephenson.

Adlard & Son, Ltd., Impr.

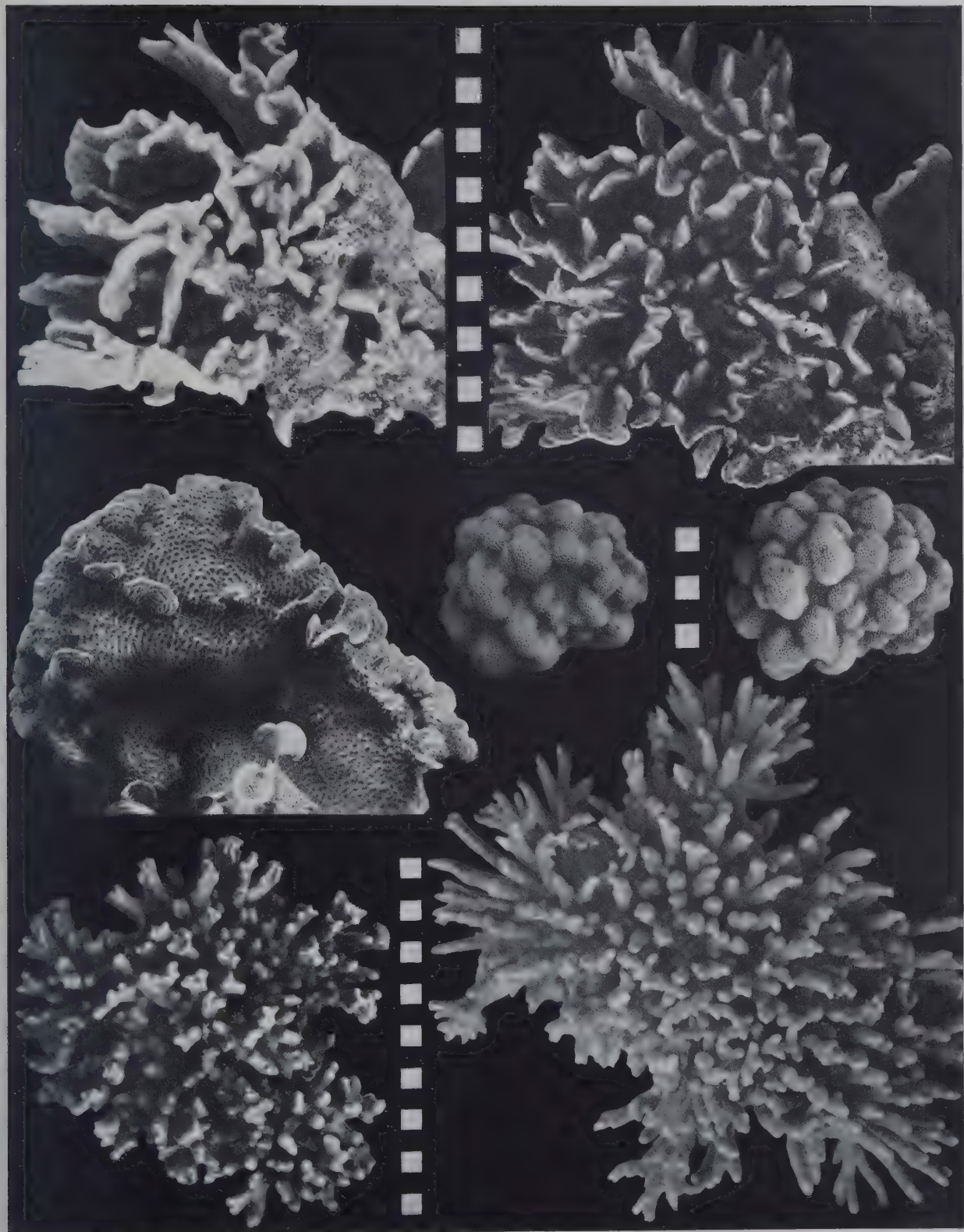
DESCRIPTION OF PLATE V.

GROWTH IN COLONIES OF PAVONA, PORITES AND BRANCHED MONTIPORA IN THE HABITATS IN WHICH THEY WERE FOUND.

FIGS. 1-3.—*Pavona cactus*. Experiment I, no. 73. Collected and planted out in the moat. This species is made up of somewhat massive vertical plates (one of which is illustrated in side view in fig. 3) with foliose margins. The specimen illustrated was part of a large colony which had shared in the formation of a platform in the western moat, part of the top of which had been killed after reaching low-water level. During the experimental period the coral not only increased in diameter (25% and 15% on two diameters in 33 weeks 1 day), but also increased the growth of small secondary plates on its upper surface (in figs. 1 and 2 it is viewed from above).

FIGS. 4 and 5.—A massive species of *Porites*. Experiment I, no. 48a. Collected and planted out in the moat. The amount of growth in this coral (an increase of 8% and 6% on two diameters in 33 weeks), is naturally much less than the amounts illustrated in Plates I-IV, because of the massive form of the coral; but is rather low compared with the increase achieved by certain other colonies of *Porites* used in the experiment.

FIGS. 6 and 7.—*Montipora ramosa*. Experiment I, no. 71. Collected and planted out in the moat. This species is one of the most characteristic of the inhabitants of the moats. Not only does it grow rapidly (the case illustrated showing an increase of 50% and 64% on two diameters in 33 weeks 1 day), but it changes markedly in aspect as it does so. From figs. 6 and 7 it can be seen that the appearance of the branches at the end of the experiment is very different from their appearance at the beginning; and from fig. 7 that the central branches are somewhat different from those at the periphery (this difference is not simply an effect of foreshortening). It would be pardonable for a worker unacquainted with the history of this colony to mistake figs. 6 and 7 for photographs of distinct species.



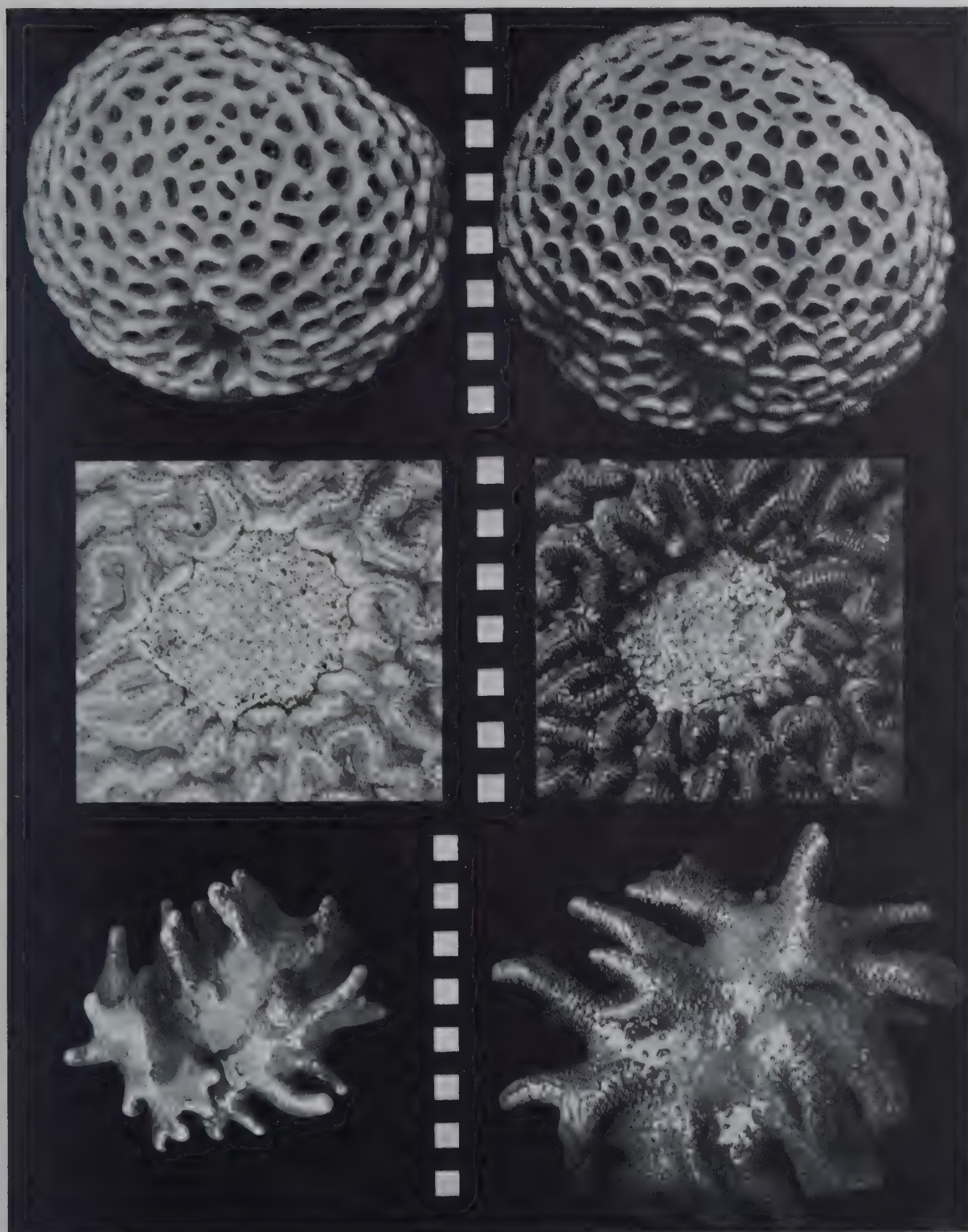
DESCRIPTION OF PLATE VI.

TO ILLUSTRATE SPECIAL POINTS.

FIGS. 1 and 2.—*Favia doreyensis*. Experiment I, no. 70. Collected and planted out in the moat. These figures illustrate the work described on pp. 191-4, in which the history of individual polyps was followed; it will be noted that the fate of each polyp can be traced clearly in the central parts of these two photographs; on original prints, larger than the reproductions, the details are well brought out. The increase in size of the colony was 8% on each of two diameters in 33 weeks 1 day.

FIGS. 3 and 4.—*Symphylia recta*. Experiment I, no. 11. Collected and planted out in the moat. These figures illustrate part of a large colony which had a dead area in the middle of its upper surface. During the experiment the living part grew inwards over part of the dead region.

FIGS. 5 and 6.—*Lobophytum* sp. Experiment I, no. 24*b*. Collected and planted out in the moat. To illustrate growth and change of form in one of fleshy alcyonaria which are common on the reef. This specimen grew well in the moat, but the latter cannot be regarded as its normal habitat.



DESCRIPTION OF PLATE VII.

THE EFFECT OF ENVIRONMENT ON GROWTH.

REGENERATION IN POCILLOPORA.

FIGS. 1 and 2.—*Acropora hebes*. Experiment II, no. B 8. Collected and planted out in the moat. This specimen is one half of a colony, the other half of which was planted in the anchorage. Both halves grew well, but the half in the anchorage was broken and could not be measured; the half illustrated increased 59% and 45% on two diameters in 31 weeks 3 days. This species is capable of rapid growth under the rigorous conditions of the moat, which is one of its normal habitats; but it grows well also in the less extreme environment of the anchorage. The aspect of the branches of the specimen illustrated has changed markedly during the experiment.

FIGS. 3 and 4.—*Pocillopora bulbosa*. Experiment II, no. A 4. Collected and planted out in the moat. Fig. 3 represents one half of a young colony which was bisected. The bisection left this half with one particularly flat side. In fig. 4 the colony has regained normal symmetry. See also p. 188.

FIGS. 5-7.—*Acropora* sp. Experiment II, nos. A 7 and B 7. Fig. 5 shows one half of a small colony which was found as a casual in the moat (it was certainly not a normal inhabitant of the latter), and which was bisected. The half illustrated was planted in the anchorage, where it grew very strongly, its appearance at the end of the experiment being represented in fig. 7. The other half, very similar to fig. 5 in appearance, was planted in the moat; its aspect after the experiment is represented in fig. 6; a certain amount of growth has taken place, but much less than in fig. 7, and the branches are all dead at the base, and some of them all the way up. If the experience of this colony is general, the inability of the species to flourish under moat conditions is clearly demonstrable.

2

6

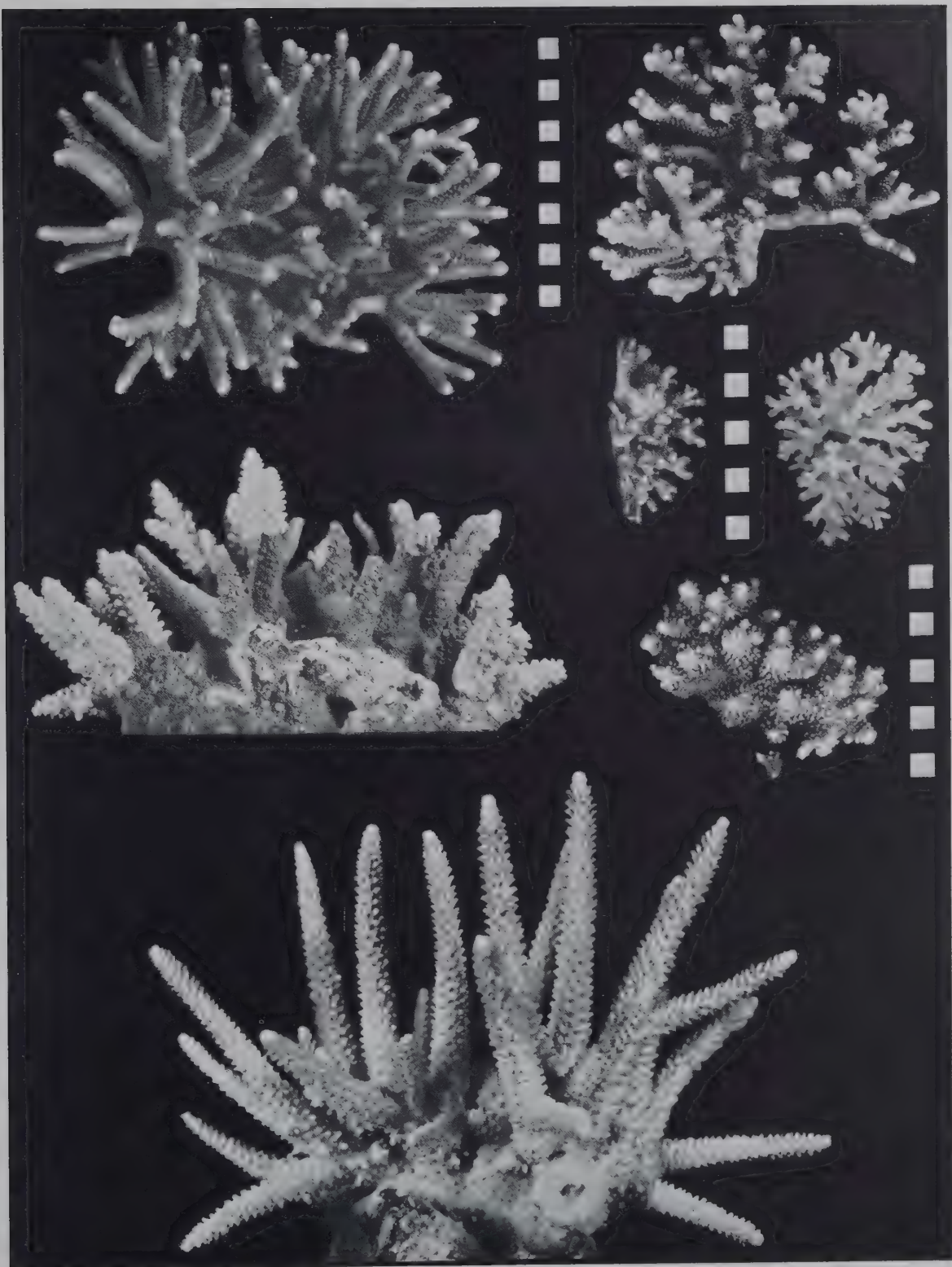
7

1

3

4

5



DESCRIPTION OF PLATE VIII.

REGENERATION IN ACROPORA.

(See also p. 185.)

FIG. 1.—*Acropora formosa*. Experiment III, no. 2. The tip of a branch which had been allowed to regenerate for 7 weeks 1 day. The broken end was still flat, but the central polyp had regenerated, and was surrounded by a ring of still smaller ones. The skeletal counterparts of these polyps are visible in the photograph. $\times 2$.

FIGS. 2-5.—*Acropora polymorpha*. Experiment III, no. 9. Stages in the regeneration of branches, all more advanced than the early condition shown in fig. 1. The point at which the fracture was made, in each branch, is indicated by a white arrow; and the stages are further described on p. 186. All four branches had been regenerating *for the same period*, viz. for 25 weeks 3 days; all belonged to the same colony and were broken on the same day; yet the amounts of new growth achieved are very different. All figures $\times 2$.

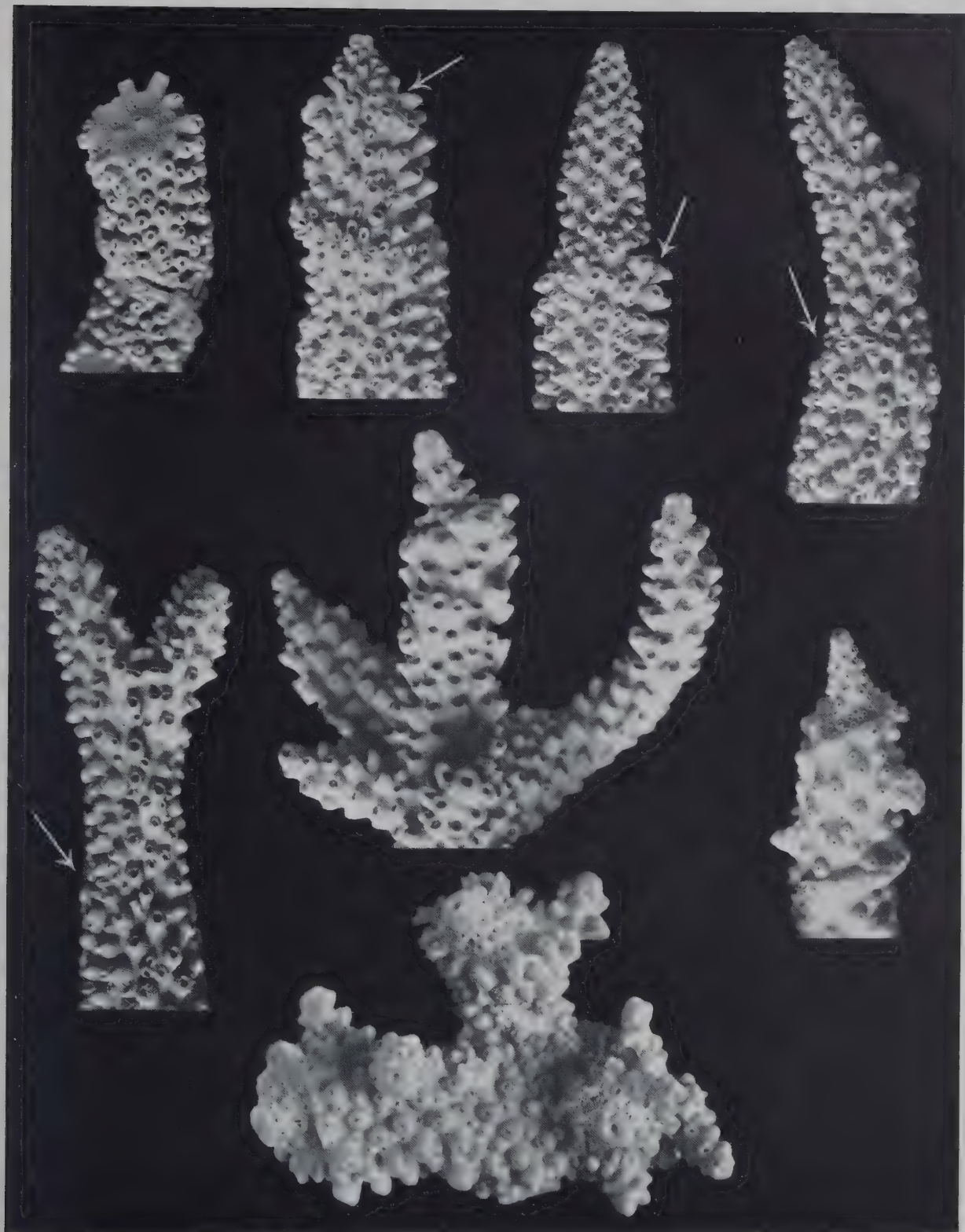
FIGS. 6-8.—These figures illustrate further details of regeneration in species of *Acropora*, and are described on p. 186. All $\times 2$. They belong to Experiment III, nos. 10, 3 and 11 respectively.

1

2

3

4



DESCRIPTION OF PLATE IX.

REGENERATION IN ACROPORA.

GROWTH-FORMS ON THE OUTER BARRIER.

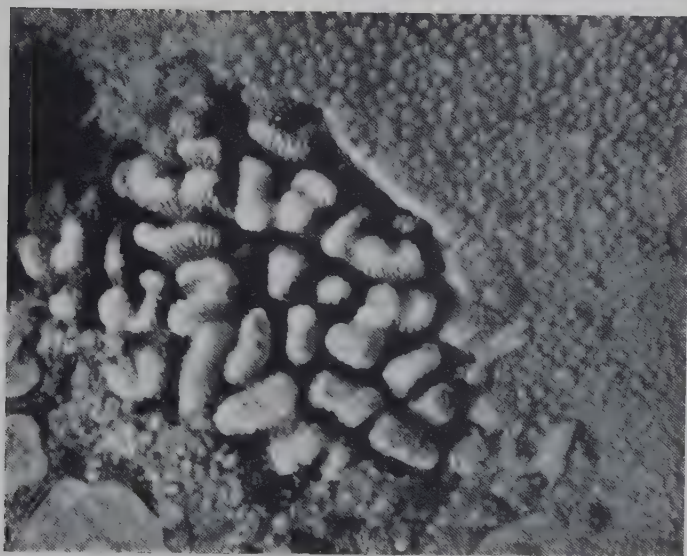
FIG. 1.—*Acropora gemmifera*. Experiment III, no. 5. A colony in which a group of branches (on the left-hand side of the figure) was broken off, the colony being left *in situ* to regenerate. The broken branches were marked by a silver wire encircling their bases (the wire is visible in places, in the figure, and has been sheathed with calcium carbonate by the coral). The broken branches, after 13 weeks 5 days, have grown new tips, but are still shorter than the unbroken branches on the right-hand side of the colony. Actual diameter of the colony 42 cm.

FIGS. 2-4.—These figures represent corals growing *in situ* on Yonge Reef, Outer Barrier. Fig. 2 was taken in the outer moat, fig. 3 near the outer ridge, both situations being exposed to strong wave-action at certain states of the tide; fig. 4 was taken on a coral head on the leeward side of the reef. Fig. 2 shows a colony of a small massive species of *Pocillopora* (*P. verrucosa*) which is very characteristic of the region, and is bright magenta in colour; and also an encrusting sheet of *Acropora* (right-hand side of figure) belonging to one of the shelf-like species, probably *A. hyacinthus*, but showing reduction of the branches in correlation with the encrusting habit. Fig. 3 shows a case of the reduction of branches to conical prominences. The species is probably *A. gemmifera*, the one also illustrated in fig. 1, which represents a colony from a sheltered habitat at Low Isles. Fig. 4 (also *A. gemmifera*) shows the variation in the form of individual branches which may occur in one and the same colony. The branches in the centre are short and conical (the effect of foreshortening in this case is relatively slight), whilst those round the edge of the colony are comparatively slender and finger-like, and are comparable to the ones illustrated in fig. 1.

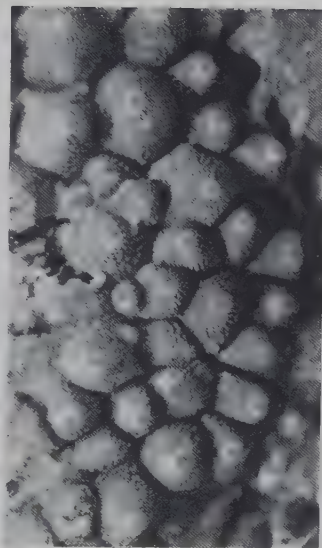
1



2



3



4

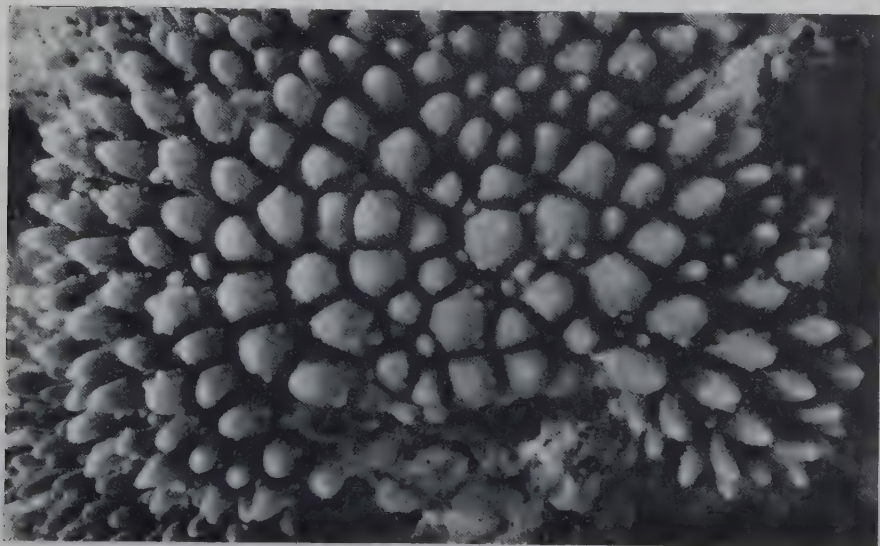


Fig. 1 photographed by F. Pittock.
Fig. 2-4 photographed by S. M. Manton.

DESCRIPTION OF PLATE X.

HABITAT AND GROWTH-FORM IN ACROPORA.

FIGS. 1 and 2.—*Acropora squamosa*. These figures represent portions collected by S. M. Manton from different sides of the same colony. Fig. 1 shows a normal branch of the species, such as would occur on many typical colonies; the branches represented in fig. 2 are so much modified that their recognition as examples of *A. squamosa* would be difficult if their origin were unknown. The colony from which both specimens were taken was growing on the reef-crest of one of the reefs of the Outer Barrier. (The manner in which two growth-forms such as these may grade into each other is shown in Plate IX, fig. 4.) These illustrate a case of marked variation in the form of branches in the same environment.

FIG. 3.—A colony (probably referable to *A. gemmifera*) with branches of an intermediate degree of stoutness. Locality unknown.

FIG. 4.—*Acropora squamosa*. From the reef crest, Yonge Reef. A good example of a squat form of the species, which has nevertheless not assumed the atypical appearance of fig. 2.

FIG. 5.—*Acropora gemmifera*. A colony with short and stumpy branches, intermediate between the conditions shown in Plate IX, figs. 1 and 3. The specimen came from the wave-washed pavement at the seaward edge of Batt Reef.

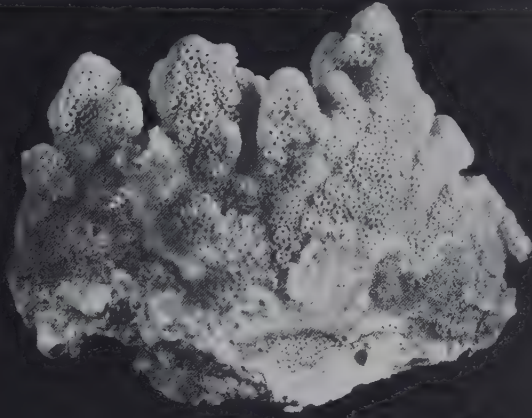
FIG. 7.—*Acropora delicatula*. From the outer moat, Yonge Reef. This species, notwithstanding the fact that its branches are so fragile that it is difficult to collect a colony without breaking it, is a form characteristic of the seaward parts of Yonge Reef, and grows on the outer ridge. Although it is commonest on the sides of clefts where the force of the breakers may be somewhat diminished, it also occurs on the open ridge, where it must at certain times receive their full force. A comparison of this figure with Plate IX, fig. 3, will show how two extremes of structure (depending for strength upon different principles) may both be successful in resisting the pounding of the surf—short cones of great strength on the one hand, which are difficult to split even with a cold chisel; slender fragile branches on the other, which snap off at the least tap from a chisel.

FIG. 6 and 8.—*Acropora hyacinthus*. Fig. 6 shows a typical slender-stemmed example of the species, growing in a sheltered habitat at Low Isles (this specimen was no. 60b in Experiment I—see also Plate II, figs. 5 and 6). Fig. 8 shows a stouter colony from the outer ridge on Yonge Reef. These two were growing therefore in habitats exhibiting something approaching the maximum possible amount of difference between shelter and exposure; yet the difference between them is not very marked.

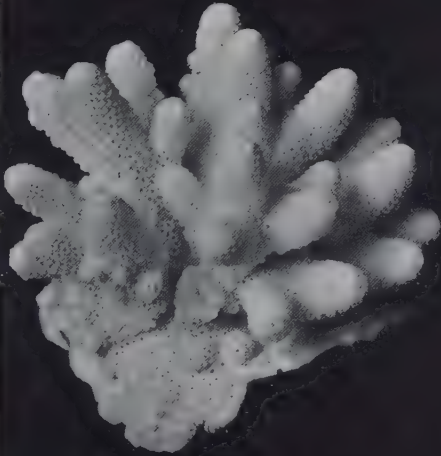
1



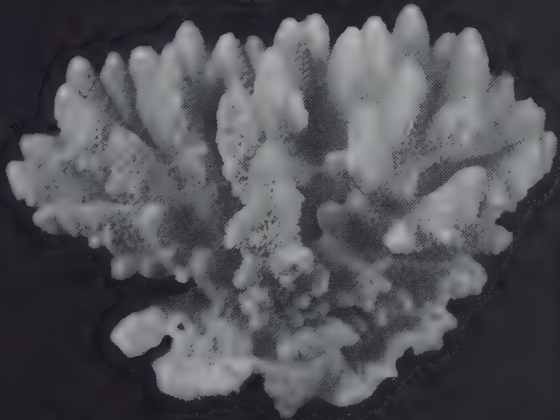
2



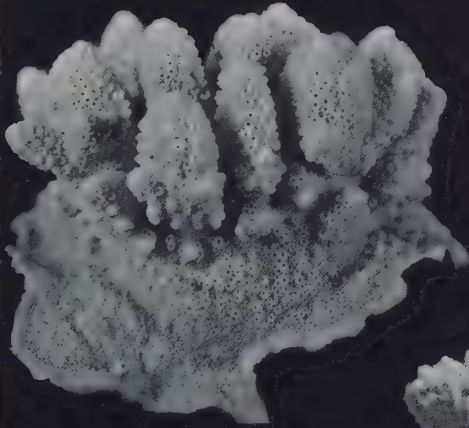
3



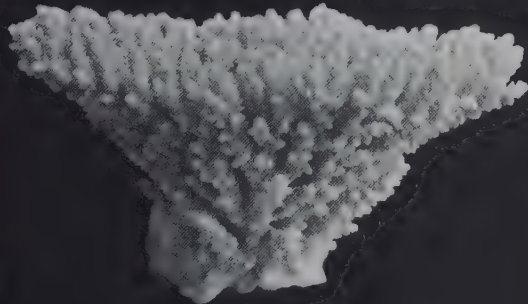
4



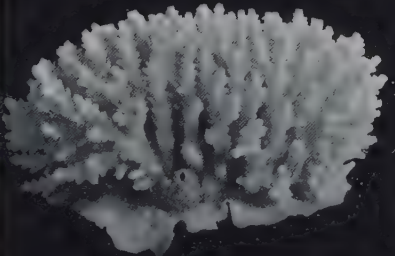
5



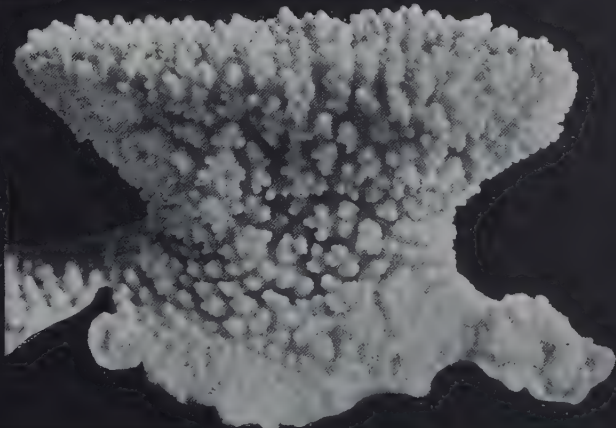
6



7



8



THE BREEDING OF REEF ANIMALS

PART I. THE CORALS

BY

SHEINA M. MARSHALL, B.Sc.,
Naturalist at the Marine Station, Millport;

AND

T. A. STEPHENSON, D.Sc.,
Professor of Zoology in the University of Cape Town

WITH SIX TEXT-FIGURES, ONE PLATE AND THREE TABLES

CONTENTS.

	PAGE
1. PREFACE	219
2. THE GONADS OF CORALS	220
3. THE LIBERATION OF PLANULAE BY CORALS	235
4. SUMMARY	241
5. TABLES	242
6. REFERENCES	243

1. PREFACE.

(By T. A. STEPHENSON.)

ONE of our objectives during our residence at Low Isles was to discover, if possible, whether in a tropical marine area of this nature, the breeding of common animals goes on fairly steadily all the year round, or whether there is a concerted breeding season for the majority of them at some particular time of year. It may be stated at the outset that our work in this direction must be regarded as a preliminary study; it *does* provide a partial answer to the question just formulated; but it sketches in the details only slightly. It will be clear to anyone familiar with work of this nature that in dealing with a considerable number of species for one year only, in the intervals of other work, a complete picture could not be expected. The next workers to take the matter up, however, should now be in a position to carry it rapidly to a more advanced stage.

The work on the gonads of corals was done by myself, both in the field and subsequently on preserved material; except that I have to thank S. M. Manton for carrying out the examination of the fresh gonads for me during two months of the year (27th April to 18th June, 1929). The work dealing with the liberation of planulae, however, was executed jointly, by S. M. Marshall and myself; and the majority of the collections and counts of planulae were made by her. In connection with this work we have to thank other members of the expedition, especially E. A. Fraser and A. P. Orr, for helping us with the collection of material. The text-figures, with the exception of Text-figs. 1 and 6, were drawn by Anne Stephenson, who also prepared some of the slides required. Other slides were made by F. C. Sherlock.

In the second part of this paper the results obtained with invertebrates other than corals will be described, by Anne Stephenson, who was responsible for that part of the investigation. The conclusions for the whole work together will there be stated.

2. THE GONADS OF CORALS.

(By T. A. STEPHENSON.)

MATERIAL AND METHODS.

It was realized at the outset that the problem of breeding in corals can be attacked from two points of view. Since most of them are viviparous, one may attempt to discover their breeding season by finding out at what times they liberate planulae. On the other hand one may examine their gonads regularly, in order to find out when these are ripe. The latter method is less straightforward in the case of corals than it is in sea-urchins and certain other invertebrates whose gonads are relatively large and readily accessible, and in which the signs of maturity are comparatively easy to read. The polyps of a coral are often so small that a study of their gonads by any method other than that of cutting serial sections is impracticable; and even in the forms with large polyps, the examination of the gonads is a somewhat lengthy process. It was decided therefore to choose certain common forms with small polyps, and to discover if possible at what times these liberated planulae; and to choose other species with larger polyps for an examination of gonads. The choice of these latter forms was practically limited, at Low Isles, to three genera—*Favia*, *Symphyllia*, and *Lobophyllia*. It was also necessary to choose species which could be obtained from pools on the reef-flat or from shallow water on the seaward slope, otherwise the supply of material would have become too difficult. As it was, the supply began to run out by the end of the year, since no one species belonging to either of these genera was particularly plentiful. The form chosen as most suitable for the principal work was *Favia doreyensis*, a species which appeared to be as plentiful as any, and which (an important factor) can usually be recognized in the field without danger of confusing it with other species. *Symphyllia recta* was studied in lesser degree, and a few details were also observed for species of *Lobophyllia*. The latter, however, have in most cases to be obtained by diving; the number of species to be found is considerable, and they are not always easily distinguished from one another; and to obtain a regular supply of any one of them would have involved much more time than was available.

Several methods of examining the gonads of these corals were tried. In the case of *Favia*, it was found that the best way is to place a colony upside down on a board, and split it into several pieces, from below, with a cold chisel. (If the splitting is done from above it results in damage to a number of the polyps.) When possible, the colony may be split into radial slices similar to those into which one cuts a cake. If the splitting is successful, each of the cut surfaces presents the following picture: The proximal part of the colony is dead, but at a certain distance below the surface it becomes green in colour because of the presence of green filamentous algae which occupy the skeleton immediately below the living flesh of the polyps. The level at which the living tissue begins is therefore sharply marked by the cessation of the green coloration. Above the green region lies a neat row of longitudinally split corallites with their polyps, each as a rule displaying two mesenteries in surface view. The mesenteries cannot contract unduly because they are attached to the skeleton; so the gonads and mesenterial filaments can be examined to advantage. The general examination was carried out under a binocular microscope, and a number of individual gonads in the fresh condition were removed from each colony for more detailed microscopic study.

Since each colony was cut into at least four, and usually six or more pieces, and since several polyps were exposed along each cut surface, the total number of gonads examined in any one colony was considerable. For instance, in an almost spherical colony whose diameter was 16 cm., and which was cut into halves, the number of vertical sections of polyps along each cut surface was 28; had this colony been divided into six equal radial pieces, the total number of such vertical sections would have been in the neighbourhood of 168; consequently the number of gonads to be seen in such a colony would have been anything up to 336. In another case the number of vertical sections exposed in six pieces which had been used for examination was counted, and amounted to 122; this would reveal a number of gonads not exceeding 244. The total number of colonies of *Favia* examined during the year was 230, and even if we take the average number of gonads examined in a colony as 100 (not a high estimate), this means that some 23,000 gonads altogether were studied. The examinations were carried out as nearly as possible at monthly intervals, though with some unavoidable irregularity. In the case of *Symphyllia*, which is harder to obtain, only 96 colonies were examined, and in that of *Lobophyllia* only 17. Colonies of *Symphyllia* were divided up in the same way as those of *Favia*; polyps of *Lobophyllia* were split up individually from below.

During the examinations a number of gonads were cut away from their mesenteries and fixed in Bouin's fluid for further study, and transferred after 24 hours to 70% alcohol. The preservation proved to be excellent. A number of whole polyps and portions of colonies were also preserved, some of these being fixed in neutral formalin and others in Bouin.

THE OCCURRENCE AND RELATIONS OF THE GONADS IN CORALS.

The gonads of corals, like those of Actinians, are situated in the mesenteries, and constitute thickenings of these. They are to be found sometimes on all the mesenteries of any one polyp, sometimes on certain mesenteries only. Although there are a considerable number of details connected with them described in the coral literature (see p. 243), yet there is no great bulk of information concerning them in existence. The present report

describes the first investigation, month by month, in the field : but still leaves many points unsettled.

In some species of colonial corals the sexes appear to be separate, whilst others are definitely hermaphrodite. In the hermaphrodite forms a single polyp may be male or female (at least at a given time), in which case it is the colony and not the individual which is hermaphrodite. In other cases each polyp is hermaphrodite, and when this is so, it may contain some mesenteries bearing ovaries alone and others which have only testes ; or all the fertile mesenteries may be hermaphrodite. Where a mesentery includes both testes and ova, these may be arranged in distinct groups, or may be intermingled.

In a species with distinct sexes, the polyps on a given colony would be all male or all female. The case of *Pavona cactus*, recorded below, appears to be an example of this ; and there are others. In examples of this kind, however, we cannot be certain that any species has separate sexes all its life, until we know enough about its life-cycle to be sure that it does not change its sex with age, or for other reasons.* The condition of a colony at a given moment is not enough to establish its status, since even in hermaphrodite forms the gametes of one sex may develop before those of the other.

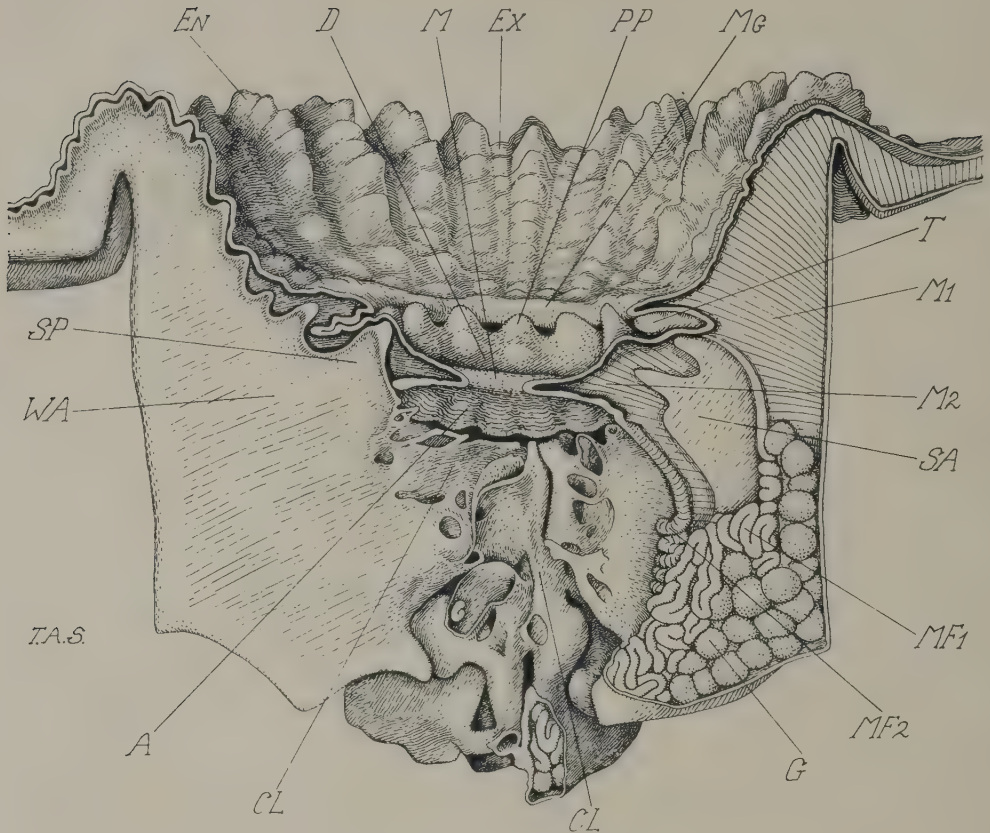
The general rule amongst corals appears to be viviparity, the fertilized egg developing into a larva before extrusion from the parent polyp ; but there are also cases in which ova and spermatozoa have been extruded as such. Whilst some of the recorded instances may have been abnormal occurrences due to special conditions (planulae being present in the polyps at the same time), there is no reason to suppose that the extrusion of sperm at least is not perfectly normal in certain species. To what extent self-fertilization occurs in hermaphrodite forms we do not know. In the case of the viviparous forms a polyp may produce one planula at a time, or a number of larvae may reach the same stage together in a single polyp.

The position and structure of the gonads in some typical corals is illustrated by the figures accompanying this paper. To appreciate the relations of the various parts involved, it is necessary first of all to obtain a clear conception of the external features of a decalcified coral polyp, and several photographs are provided on Plate I which bring out the points at issue. In fig. 1 there are shown several living polyps belonging to a simply constructed coral (*Euphyllia glabrescens*). Here one sees, below the knobbed tentacles, which are only partly expanded, that portion of the column wall of the polyp (the *edge-zone*) which overlaps and extends down the outside of the skeletal cup. This edge-zone, in *Euphyllia*, is smooth, and has a sharply-defined lower margin, below which the rough and encrusted skeletal stalk is to be seen. In figs. 2 and 3 a single polyp of *Lobophyllia*, decalcified, is represented from two points of view—from underneath in fig. 2, more from the side in fig. 3. In this case the tentacles of the polyp are retracted and are therefore not visible ; but the edge-zone is much in evidence, as a prominent saucer-like extension of the body. The spine-like processes which bound its upper margin are hollow extensions of the column-wall which fitted over actual spines in the skeleton, and are characteristic of the genus. Within the edge-zone is the conical body of the polyp, that part which occupied the skeletal cup during life. This conical portion is provided with deep longitudinal grooves, and into these the

* A particularly interesting study of a large series of polyps of *Flabellum rubrum* is described by Gardiner (1902). The facts recorded appear to justify the conclusion that in this species the polyp is male when it first reaches sexual maturity, subsequently becomes hermaphrodite, and afterwards female ; after the female phase it probably dies.

septa fitted before decalcification. At the apex of the cone is a sponge-like region consisting of membranous lamellae which occupied the interstices of the columella during life. The fertile portions of the mesenteries are contained in the lower parts of the ridges which intervene between the septal grooves. Fig. 4 shows a view, from underneath, of a larger polyp of *Lobophyllia*, which had two mouths and which had become slightly meandrine in shape; the effect of these modifications on the form and arrangement of its parts is demonstrated by the figure. The same process has been carried further in the fully meandrine species (*Symphyllia recta*) illustrated in fig. 5. Here a portion of a colony, instead of a single polyp, is represented, and the edge-zone, which is now limited to the margin of the colony, is not included in the part photographed. That part of the polyp which, in figs. 2 and 3, formed a simple cone, now has the aspect of a winding mountain-range separated by a deep valley from the corresponding part of the next polyp; but the furrows which originally contained the septa, and the ridges which contain the gonads, are plainly visible, although their arrangement is different. Lastly, in fig. 6 are seen the undersides of a number of decalcified polyps of *Favia doreyensis*. Here there is no meandriform modification, the simple individual polyps being united by a common sheet of tissue. In each polyp the grooves and ridges, the latter uniting centrally in an intra-columellar tangle of lamellae, are arranged as in *Lobophyllia*, though in this case the body of the polyp forms a pillar with a conical or more or less flattened lower end, instead of a simple cone as in *Lobophyllia*. Between the several polyps, the intermediate sheet of tissue which unites them is also grooved where it fitted, during life, over skeletal ridges.

The internal structure of the polyps of *Favia doreyensis* is illustrated in Text-figs. 1 to 5. Text-fig. 1 is an enlarged view of a single polyp divided vertically in half. The section passes on one side through one of the inter-septal alcoves which contain the mesenteries, and shows a mesentery with its gonad and mesenterial filament, and the relation of the intra-columellar tissue to the other parts; on the other side it passes through one of the fissures from which a septum has been dissolved away, and so reveals, in surface view, the wall of one of the inter-septal alcoves. Text-fig. 2 is a transverse section through the lower part of a similar polyp, and shows some of the central intra-columellar laminae, from which radiate alcoves of the coelenteron containing gonads and mesenterial filaments. It is noteworthy that the gonads in this part of the polyp are very bulky in proportion to the capacity of the coelenteron, and occupy a high proportion of the available space. The relation of parts in this section represents almost exactly the relations which obtain in a living polyp, since the body-wall in this region is firmly attached to the skeleton during life, and does not contract away from it during fixation, so that the natural proportion of the parts is preserved. Only that part of the polyp which lies above the skeleton, distal to the gonad region, can expand freely and so increase the size of the coelenteron; and in the species in question it does this only at night, remaining fully contracted in daylight. It will be further noted that in Text-fig. 2 no mesenteries are to be seen. This does not mean that they are absent, but that in this part of the polyp the bulk of the other organs is so great that they appear insignificant, and cannot be seen under a low magnification. Their presence, arranged in a typical manner, is shown in Text-fig. 3, which passes through a similar polyp distal to the fertile region. In Text-fig. 4 a single gonad is represented in detail. Here ova and testes are present, intermingled; and their finer structure is described on p. 229.



TEXT-FIG. 1.—*Favia doreyensis*. One half of a vertically divided decalcified polyp. The polyp is contracted, and the tentacles are, therefore, withdrawn, being concealed under the indrawn margin of the column. On the right side of the figure the cut passed through an exocoel, revealing an imperfect mesentery with gonad and mesenterial filament; the membranous covering of a small septum; and part of a perfect mesentery (attached to the throat) with its filament. On the left the cut passed through the fissure formerly occupied by a large septum, and thus reveals the wall of one of those alcoves of the coelenteron which lie between the septa. This figure should be compared with Text-figs. 2 and 3, and with the text, p. 223. In the gonad the eggs alone are represented, since the testes were too translucent to be accurately defined on this scale. *A*, throat (actinopharynx); *CL*, membranous lamellae of the columellar region; *D*, disc (peristome); *EN*, a crest of the column wall bounding an endocoel, and previously occupied by a septum; *EX*, a strip of the column wall bounding an exocoel; *G*, gonad; *M*, mouth; *M1*, imperfect mesentery; *M2*, perfect mesentery; *MF1*, the mesenterial filament belonging to the imperfect mesentery; *MF2*, the filament belonging to the perfect mesentery; *MG*, upper margin of column; *PP*, hollow process of the peristome which previously covered the paliform lobe of a septum; *SA*, the fold of body-wall which previously enclosed a small septum; *SP*, that part of the fold *WA* which covered the paliform lobe of a septum; *T*, tentacle; *WA*, one half of the fold of body-wall which covered a large septum; the cut edge of this fold is toothed where it followed the serrate outline of the septum. $\times 12$.

FAVIA DOREYENSIS.

FRESH MATERIAL.—The first of the 230 colonies examined were collected on 14th August, 1928, and the last on 18th June, 1929. There is thus a gap of two months in the year's record, but since it can be shown that this gap lies at the end of that part of the year during which the gonads were quiescent, it is probable that little more would have been discovered had it been bridged. The greatest diameters of the colonies used varied from 5·6 to 22·0 cm., the average being 13·7 cm. The majority were collected in the Western Moat, the others in adjacent parts of the Moat and in the Anchorage.*

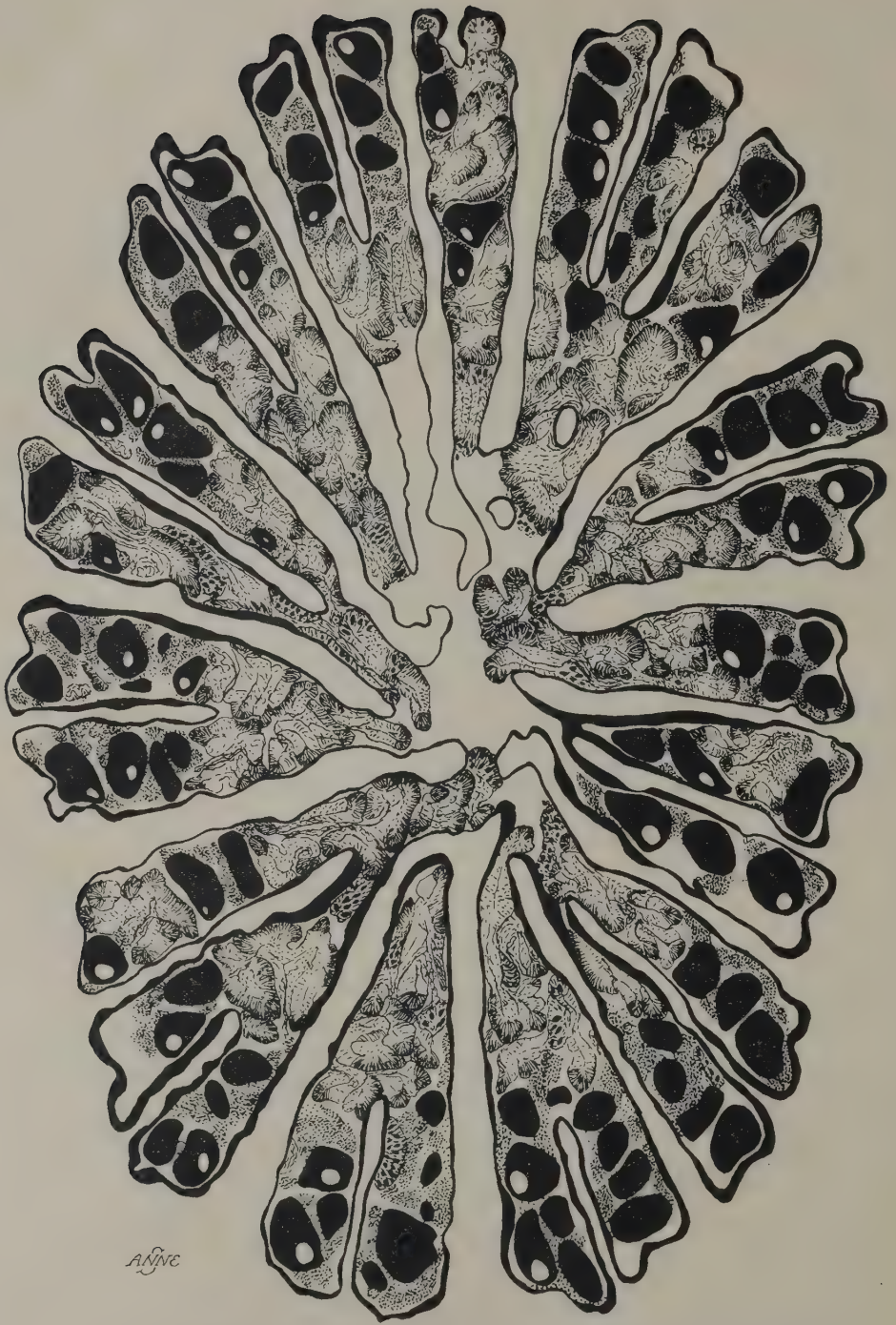
First of all it appears that, although the condition of the various gonads in a colony is not absolutely uniform, and in certain cases is somewhat variable, yet on the whole there is a fair degree of uniformity between them, so that as a rule the polyps of the whole colony are ripe or unripe together.

In the third week of August, six of the 26 colonies examined contained no gonads visible under a binocular. This means that although germ-cells may have been present in the mesenteries, they were in so undeveloped a condition as to make no appreciable swelling such as would be externally visible. In the other colonies gonads were visible; sometimes a few only could be seen, in other cases they were numerous; but in nearly all cases they were small and showed no signs of maturity. The gonads were from less than 1 mm. to 2 mm. in length, were colourless, pale green or pale blue, and contained a small number of immature ova. In one colony many of the gonads were larger than the rest and contained more eggs; and some of the eggs, usually the largest, were grey in colour instead of pale green.

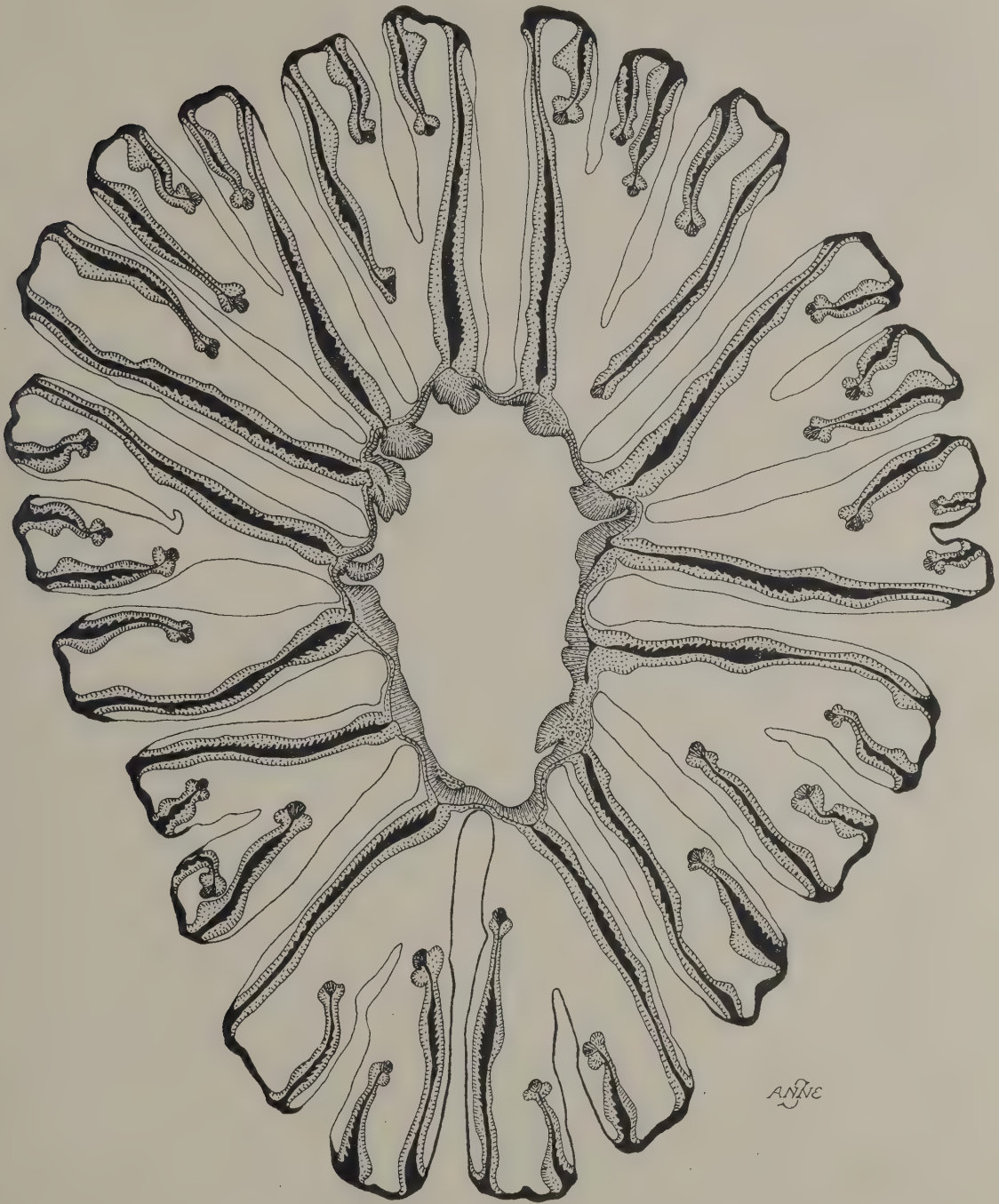
In the second week in September, the 24 colonies examined showed no advance on those studied in August; in fact not one of the September colonies showed gonads as well developed as those of the colony mentioned at the end of the last paragraph, although immature eggs were usually recognizable. Colonies with no visible gonads were fewer than in August (3), but when gonads were present they varied in length from 0·5 to 2·25 mm. and were still very immature, pale green or blue-green in colour, and as before were few in number in some colonies and numerous in others.

Examination of 24 colonies towards the end of October and during the first two days of November still showed six colonies in which no gonads could be seen; but in the remainder the gonads were usually numerous or very numerous, and were in the main considerably more advanced than those examined in September. The colour of these gonads varied from pale green or blue-green to bright pale blue, greyish, or grey and green; the size from 1 to 3·2 mm.; and this time they were often relatively large and plump. The eggs were now frequently large, and were coloured quite definitely, opaque blue, purplish-grey, etc. Among the eggs were often to be seen smaller translucent sac-like testes, from some of which fully-formed active sperms could be extracted. The sperm has an acorn-shaped head, and a long tail. In other cases the testes were not sufficiently well developed to be demonstrable. This was the first time that the presence of testes in the gonads had been ascertained. In August and September none of them were seen, though they may have been present in an immature condition.

* These localities are marked on the map of Low Isles given in Vol. III, No. 2, of these Reports, Plate I.



TEXT-FIG. 2.—*Favia doreyensis*. Transverse section of a polyp, passing through the fertile region, and below the throat. The outline of the section is deeply indented by the fissures originally occupied by septa; and some of the lamellae of the columellar region are visible in the centre. The ova are black, their germinal vesicles white; the testes are stippled, and the mesenterial filaments, the bulk of which lie nearer the centre than the sex-cells, are shaded with strokes.
 × 31.



TEXT-FIG. 3.—*Favia doreyensis*. Transverse section of a polyp passing through the throat and above the fertile region. There are 24 pairs of mesenteries, whose endocoels are occupied by folds of the body-wall which previously covered 24 septa. In the throat and mesenteries the mesogloea is black, the endoderm stippled and shaded with short strokes, the ectoderm shaded with long strokes; in the body-wall the whole thickness is represented in black, as the three layers are too thin to be treated individually. $\times 31$.

During the three days 29th November to 1st December, a further 24 colonies were examined. Five of these had no visible gonads; in the others the gonads were usually fairly or very plentiful. This time again the eggs were often large,* and appeared to be very well developed, but were not readily liberated by the gonad - *i. e.* they did not float out of it as so often happens with the mature eggs of invertebrates. Their vesicular nuclei were usually clearly visible, even under the binocular, and the egg was crowded with small fluid spheres of perfectly regular form, which were completely free from one another, and streamed out of the egg if its membrane were ruptured (these details had been observed in earlier examinations also). The advance on the last month, however, seemed to lie mainly in the fact that in all the colonies which had gonads at all (save one) the presence of fully or almost fully formed, often active sperms was demonstrated: but the sperms did not readily leave the testes, and when motile were only moderately active. The condition of the gonads just described led to the supposition, on the analogy of previous experience with other invertebrates, that although the gonads were maturing, they would not be ready for spawning for some little time. As the sequel will show, however, the spawning must have actually taken place during December, and perhaps also partly during November.

From the beginning of January onwards, until the middle of June, the results were entirely different. The number of colonies examined during these months was 132, and of these 99 had no visible gonads whatever. In the remaining 33 colonies there were present, usually in comparatively small numbers, very slight transparent or whitish patches or ridges on the mesenteries, occupying the proper position for gonads, and sometimes as much as 1 mm. or a little more in length (though commonly less), but very slender, and containing no recognizable eggs or sperms. In other words, there were the rudiments of gonads, containing more or less undifferentiated cells only. These undeveloped gonads were more plentiful in June than in any of the preceding months, suggesting that the corals were beginning to become sexually active once more, and would be ripening during the later months of the year, as was the case with those examined in the preceding year.

The indication of the facts recorded in the above paragraphs seems clear enough. Although the spawning was not actually witnessed, it appears evident that the gonads were ripening from August to the end of November, that spawning occurred in December (early summer), and that the gonads then died down into a rudimentary condition, or ceased to be externally visible on the mesenteries altogether, remaining in such condition until mid-June, when there were slight signs of renewed activity.

It will have been noted that even in the months during which the gonads of the great majority of the colonies were ripening, there were always a few colonies which showed no signs of sexual activity at all. Of the 98 colonies examined during the maturing period, 63 were more than 10 cm. in diameter, the remaining 35 measuring 10 cm. or less. Of the colonies larger than 10 cm., 48 had more or less *numerous* gonads, and only 4 had none at all: whereas of the colonies with diameters of 10 cm. or less, 16 had no visible gonads, and in the rest, although gonads were present, they were recorded as *numerous* only in 4 colonies. In the case of 18 colonies in which the gonads were either few or not very numerous, the average diameter was 10.7 cm., these forming an intermediate group with

* Measurements of eggs preserved during these three days are as follows: Greatest diameter of ovum, 305-374 μ ; greatest diameter of germinal vesicle, 87-126 μ ; diameter of the principal nucleolus, 17-37 μ .

some of its members on either side of the 10-cm. line. There is a distinct size-effect here, suggesting that on the average, colonies of this species begin to be strongly fertile only when their diameter has reached a figure in the neighbourhood of 10 cm.

It would also appear that a coral gonad advertises its maturity in a somewhat less distinct fashion than the gonad of many other invertebrates. In these latter one may expect the eggs to wash out more or less freely from a cut gonad when it is ripe, and may expect the sperms to show a very high degree of activity. The coral gonads never reached this condition so far as the recorded observations went.*

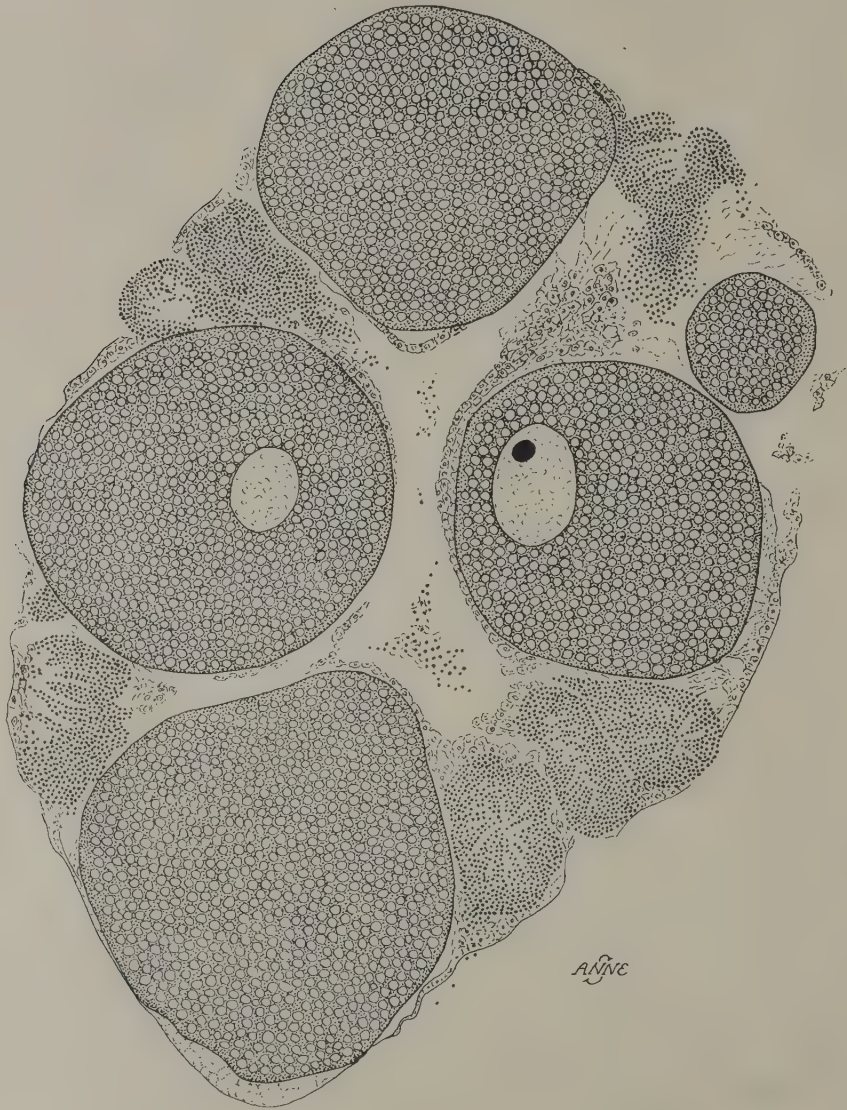
PRESERVED MATERIAL.—Serial sections of a considerable number of isolated mature gonads were prepared. The stain used (iron haematoxylin) gave excellent results. In addition, series were made of two entire polyps, some of these being stained with haematoxylin and eosin, others with iron haematoxylin and light green.

The egg of *Favia doreyensis* (probably similar to that of many other corals) might make a very favourable subject for cytological study, because it is not only unusually large, but has also reasonably translucent contents. A typical mature egg of this species (Text-figs. 4 and 5) is spherical, subspherical or ovoid in shape, or is sometimes of less regular form. The cytoplasm is evenly packed with those spheres which were described above as characteristic of the living egg. The spheres themselves appear as cavities in the sections, but the cytoplasm between them stains lightly, and contains many small granules, probably of several kinds. Immediately below the surface of the egg there is a distinct cortical layer free from the above-mentioned spheres: and outside this a thin layer of mesogloea. The nucleus is large and vesicular, and lies at one side of the egg just below the surface, which it may slightly bulge outwards. One side of it is in contact with the cortical layer of the egg, or in cases where it lies just below the general level of the cortex, the latter dips inward a little to meet the nucleus. The nucleus contains a network dotted with fine strands and granules. It possesses a single large, spherical, eccentrically placed nucleolus, which is itself granular in structure. In addition to this there are several (3-6 in the cases counted) small subsidiary nucleolar bodies: and similar bodies sometimes occur in the cytoplasm just outside the nucleus, possibly representing material which has been extruded from the latter. *The egg contains no zooxanthellae.*

Testes, which are mixed up indiscriminately with the ova, lie sometimes peripheral to them and sometimes between them, tending to occur in groups, and are much smaller than the eggs. They consist of sacs of various shapes and sizes, containing numerous sperms. The tails of the sperms converge towards one end or one side of the sac, whilst their heads lie in radiating groups, and also occupy much of the peripheral part of the testis. In many gonads free sperms are to be found, which have escaped from their testes, and which lie between the ova. Since ruptured ova with the contents streaming out also occur, the liberation of these sperms from the testes may be entirely artificial. At the same time the testes are evidently in an easily ruptured condition.

The gonads whose structure has just been described were all preserved from 29th November to 1st December, 1928. The study of the fixed material supports the view already taken of the fresh, that the gonads were ripe or very nearly so at that time. Some further gonads, from a colony examined on 1st November, were also sectioned. These were in much the same condition as the ones preserved a month later.

* Probably the eggs are dehiscid through temporary openings in the endoderm of the gonad; but this was not actually seen.



TEXT-FIG. 4.—*Favia doreyensis*. Section of a mature gonad, fixed on 30th November, 1928, passing through five ova and several testes. The section cuts the nuclei of two of the eggs, and these nuclei come in contact with the egg-cortex in other sections of the series, as in Text-fig. 5, *B*. The heads of the sperms are represented by dots, but they are shown as being less numerous than in reality, for the sake of clearness. Some of the testes have ruptured, and sperms have escaped into the tissue-spaces. The tissue of the gonad is in a reduced condition. $\times$ ca. 170. Slightly diagrammatic.



TEXT-FIG. 5.—*A*, *Symphyllia recta*; *B*, *Favia doreyensis*. An egg of each species, the two represented to the same scale ($\times$ over 300). The details of egg-structure are described in the text, pp. 229 and 233. The figures are slightly diagrammatic.

SYMPHYLLIA RECTA.

FRESH MATERIAL.—In the case of this species it was only possible to examine 96 colonies, at the rate of 12 a month, for 8 months. These colonies were obtained mostly from the Anchorage, a few from the Western Moat. Their average size (greatest diameter) was 18.5 cm., the smallest colony measuring 8.1 and the largest 28.0 cm.

As in the case of *Favia doreyensis*, a proportion of the colonies possessed no visible gonads at all: but of such colonies there were only 28, the remaining 68 having at least some trace of gonads.

In August only one of the 12 colonies examined had any trace of gonads; and in that colony only a single distinctly formed gonad could be found, this containing a few immature ova.

In October seven of the 12 colonies showed at least some signs of activity. In one of these, only a single small gonad with indeterminate content could be seen; in three other colonies young ova were found, but were present in very few mesenteries. In the remaining three colonies the gonads were better developed and fairly numerous, but had no decided colour. In the first of these colonies there were numerous eggs of various shapes and sizes, the larger ones measuring 240–415 μ in diameter (when very slightly crushed by a cover-slip). Most of these eggs were translucent, and the nucleus was sometimes visible; but one was larger and opaque salmon in colour. Immature testes were probably present. In the second colony some of the gonads consisted of two quite distinct packets of eggs, one packet containing young colourless ova, the other containing much larger opaque salmon ones, well rounded and apparently mature, each with a translucent nucleus. In the third colony there were young ova, but very few of the larger salmon-coloured ones. In no colony were sperms identified.

In December the gonads of 12 further colonies were either absent or present in a rudimentary condition, the content being undifferentiated. Such gonads appear as slight translucent whitish spots or thickenings on the mesenteries, varying from 0.5 to 2.2 mm. in length.

During January, February, March and April, 48 colonies were examined. Only three of these were in so reduced a condition that no traces of gonads could be found; but in the rest, although there was at least some slight indication of gonads, only in two cases were these sufficiently well developed to contain determinate ova. The rudimentary gonads were often numerous. No testes or sperms were seen.

In May a slight increase of activity was observed, since in this month six of the colonies had yellow or yellowish-white gonads in which ova were present; and in one colony there were probably immature testes also. The gonads were fairly numerous in two of these colonies.

This scanty record provides little basis for any conclusion. So far as it goes, it appears to show that from December to April the gonads are in a quiescent condition. Signs of activity were found in October, possibly pointing to a spawning period in November, which would be close to that of *Favia doreyensis*. On the other hand there were formed gonads to be found in May also.

PRESERVED MATERIAL.—Serial sections of several gonads were cut, taken from a colony examined on 28th March, 1929; and in which ova of various sizes had been demonstrable in the fresh condition, the gonads being numerous and pale salmon in colour.

These sections, stained as before with iron haematoxylin, show a variety of ova which, though not as large as those of a mature *Favia* or *Symphyllia*, are nevertheless of considerable size (Text-fig. 5). The greatest diameter of the larger ones measured varies from 188–335 μ ; the diameters of their nuclei from 54–100 μ ; of their nucleoli from 14–23 μ . The shape of the eggs varies considerably; they are often much larger in one diameter than in the other, and may be of curious forms, possessing processes which make their outline irregular. The germinal vesicle is large, usually with well-defined and deeply-stained strands of chromatin. The nucleolus is large and spherical, and contains a clearly visible internal network in which there is sometimes a transparent vesicle. The cytoplasm includes alveolar spheres, as in *Favia*: and the substance occupying the intervals between them stains lightly, and includes a variety of fine granules with different staining properties. The spheres are somewhat smaller than in *Favia*. The surface of the egg is sometimes fairly well defined, sometimes less so. The superficial layers of the egg vary somewhat in appearance from one part of the egg to another. There is a cortical layer of variable depth, which has the character of an open network, contrasting with the darker, more solid-looking cortex of the *Favia* eggs. Below the cortex there is in some places a layer in which the alveolar spheres tend to be fewer. There occur in and somewhat below the cortex (and to a limited extent scattered through the cytoplasm) two kinds of unusually large and conspicuous granules. Some of these are stained grey, others black; or part of a granule may be grey and the rest black, suggesting that the two kinds of granule are phases of a single type. These granules may be very abundant in some parts of the circumference of the egg, scanty or absent in other parts, and typically the black ones form a conspicuous belt round one arc of the egg, being almost or completely absent from the opposite side. A similar arc of black granules may be found in some *Favia* eggs, but here they are smaller.

The state of affairs just described suggests, what would be expected on other grounds, that these eggs are less mature than the ones described under *Favia*, being in an earlier phase of their growth-period. No testes are to be distinguished in these gonads.

LOBOPHYLLIA.

FRESH MATERIAL.—In the case of *Lobophyllia* the data obtained are so few that they provide very little indication as to the time of the breeding season; besides which they apply to at least three distinct species. From the point of view of the structure of the coral gonad, however, they provide interesting information.

The 17 colonies examined were mostly obtained by diving, in or near the Anchorage. Three of them came from Batt Reef. Their greatest diameters varied from 10·7–22·0 cm. or more, the average being more than 16 cm.

The state of the gonads in these colonies was as follows:

(i) Eleven of the colonies, belonging to two species, were examined on 6–7th December, 1928. These either had no visible gonads at all, or else possessed rudimentary ones in which neither ova nor testes could be demonstrated, though in some cases the content was more differentiated than in others. Another colony examined on 9th February, 1929, had also rudimentary gonads.

(ii) One colony, examined on 2nd November, 1928, was heavily laden with eggs, which appeared to be well on the way to maturity, and had clearly visible nuclei. Their

diameters were of the order of 270μ . The gonads were salmon coloured, large and stout (5.0 to 8.6 mm. in length), but neither testes nor sperms could be found.

(iii) Another colony examined on the same date was in much the same condition as the one last mentioned, but in some of the gonads there was a small area (at the end of the gonad nearest the polyp's mouth) containing follicles which appeared to be immature testes.

(iv) A third colony examined on the same date was in a very interesting condition. To begin with, numerous active sperms were extracted from it, whose structure could be clearly observed with the assistance of dark-ground illumination. The gonads usually contained both ova and testes, but sometimes testes only. Many of the eggs were large and salmon-coloured, often with the nucleus clearly visible. The riper testes consisted of bulky cream-coloured tissue, with a milky appearance. The relation between ova and testes varied considerably in different mesenteries; usually there were testes above and ova below; sometimes the two occurred intermingled. The testes occupied much more space than the ova, and apparently often included both ripe and unripe follicles. The shapes of the riper follicles were indistinct, and they appeared milky and contained numerous sperms; the shapes of the less mature follicles were more distinct, and these were translucent and colourless. Packets of immature follicles often occurred at the upper end of a gonad.

(v) A colony examined on 22nd October, 1928, had numerous large gonads, brownish-salmon in colour (5.0 to 5.5 mm. in length), which were universally distributed in the colony. The larger ova measured 350μ , etc., in diameter (slightly crushed by cover-slip). There usually occurred, above or beside the upper part of the ovary, a packet or packets of tissue of different texture, sharply marked off from the riper portion of the ovary. This tissue sometimes contained much younger eggs, but appeared in most cases to consist of immature testes. The presence of sperm in this case could not be certainly ascertained.

(vi) It will be noted that the four colonies just described were all in a more or less mature condition in late October or early November. The only other colony examined which had well-developed gonads was studied on 24th August, 1928, and had large (4 mm.) salmon-yellow gonads containing ova of various sizes.

PAVONA CACTUS.

On the early morning (about 5.30 a.m.) of 30th November, 1928, a large colony of this coral, situated in the Western Moat, was seen to be slowly emitting milky clouds into the water. Two separated pieces of the same colony, which had been removed from the main portion and mounted on cement blocks in an adjacent pool (in connection with a growth experiment) were doing the same. Samples of the milky clouds were collected and centrifuged, and were found to contain numerous active sperms.

A group of seven polyps from one of these colonies was cut into serial sections. All these polyps were fertile, and none contained ova. In all of them there were (a) groups of cells which appeared to be spermatogonia, (b) testes (or parts of testes) containing numerous formed spermatozoa, and (c) testes which were partly empty and which appeared to have shed some of their contents. If the empty appearance of these testes is not an artefact (which I think improbable), it seems to indicate that the polyps to which they belonged were some of those which had actually been emitting sperm at the time when they were

fixed. The presence of numerous unshed sperms makes it evident that spawning was not finished, and the spermatogonia indicate a further crop of sperms yet to come. The spermatozoa appear to escape from the testes through temporary openings in the endoderm. The histological condition of these polyps is also curious: the tissues include very large numbers of gland-cells of several types, which, judging from their turgidity, must have been in an active state: and the coelenteron contains considerable quantities of a substance which seems to be coagulated fluid with an affinity for haematoxylin.

These facts make it probable that the colony in question was a male one: but without sectioning hundreds of polyps and following the history of the colony for a considerable period, it would be impossible to be certain. It is not impossible that the cells which I take to be spermatogonia might be oogonia: but as far as I am able to judge, this is not the case.

3. THE LIBERATION OF PLANULAE BY CORALS.

(By S. M. MARSHALL and T. A. STEPHENSON.)

The species chosen for this work included four branched forms—*Montipora ramosa*, *Acropora hebes*, *Psammocora gonagra*, and *Pocillopora bulbosa*: together with two massive species, *Porites haddoni* and *Favia* (*Goniastrea*) *pectinata*. The general plan with these forms was to collect either whole colonies, or branches from a number of colonies, at regular intervals, and to count any planulae which these might liberate. In practice the treatment had to be varied according to circumstances, and much more work was done on *Pocillopora* and *Porites* than on the other species. The details are as follows.

MONTIPORA RAMOSA. ACROPORA HEBES. PSAMMOCORA GONAGRA AND FAVIA PECTINATA.

The collections of these species were all made in the principal moat at Low Isles (the stretch of moat starting at the Western Moat and passing through the Middle and Fungia Moats to the Madrepora Moat). They covered the period 13th August, 1928, to 20th June, 1929; but we could not make enough of them to enable us to draw any conclusion. Since, however, over 50 collections were made altogether, and since not a single planula was obtained from any of these species on any occasion, it seems to be worth recording the dates upon which the negative results were obtained, so that they may form a starting-point for further work. It is a possibility that, at least in the cases of *Montipora* and *Acropora*, the records were all negative because these corals had been sterile all their lives, and would only become fertile once, all together, at a particular time, after which they would die. Evidence was obtained (and will be presented elsewhere) suggesting that an extensive growth of certain species of coral will spring up in a suitable locality, flourish for a time, and die out somewhat abruptly. That such a growth may breed before its extinction has been supposed by other workers, for instance Gardiner (1902, p. 470), who expresses a belief that "the ripening of the generative organs of a large number of polyp colonies of the same species in a single locality or habitat, followed by the subsequent death of all these colonies, is a regular phenomenon, ..."

The method followed, as a rule, in making collections of the branched forms, was to break off some branches from a colony and put them into a screw-topped jar of sea-water for transport to the island, samples from 12 different colonies of each species being taken in this way on each occasion. On arriving at the laboratory, the contents of each jar were placed in a separate finger-bowl of sea-water, so that, had any planulae been liberated, it would have been possible to tell which colonies had produced them. In the case of *Favia* entire small colonies were used. The collections made, therefore, represented a number of coral colonies in the neighbourhood of 600. The dates on which the collections were made were as follows :

Montipora ramosa.—1928 : 13th August ; 4th November ; 11th December. 1929 : 7th, 25th, and 31st January ; 12th February ; 12th and 24th March ; 11th and 23rd April ; 9th, 17th, and 22nd May ; 7th and 19th June.

Acropora hebes.—1928 : 24th August ; 4th November ; 12th December. 1929 : 7th and 25th January ; 12th February ; 12th and 24th March ; 11th and 23rd April ; 9th and 22nd May ; 7th and 19th June.

Psammocora gonagra.—1928 : 24th August ; 4th November ; 11th December. 1929 : 7th January ; 12th February ; 12th and 25th March ; 11th and 24th April ; 9th and 23rd May ; 8th and 20th June.

Favia pectinata.—1929 : 25th and 31st January ; 13th February ; 12th and 25th March ; 12th and 24th April ; 9th and 23rd May ; 8th and 20th June.

PORITES HADDONI.

The development of the planulae of this species has been described in an earlier report (Vol. III, no. 3) ; and it was there mentioned (pp. 129 and 130) that we cannot be certain that all our *Porites* planulae belonged to the same species. Since the identification of *Porites* species in the field is probably impossible at the present time, and since the limits of specific variation within the genus are still a matter of personal opinion, it is very difficult to speak with any assurance. On the other hand our material all came from the principal moat, and presented no variation in general form or texture which need be taken as constituting a specific distinction. The planulae which were reared all developed in the same manner, and presented identical details of structure and arrangement of parts. In a genus such as *Porites*, one might expect that in the early stages, if anywhere, differences of a specific nature would be particularly apparent ; we therefore assume for the present that we were dealing with one species only.

The first production of planulae by *Porites* was noticed by C. M. Yonge on 26th January, 1929, when a single colony in an aquarium produced several dozen of them overnight. Colonies brought in from the reef on that date were also producing them. From that time onwards material was collected every few days until 10th June. The longest gap between collections, during this period, was 12 days, and usually was much less, over 30 collections, including hundreds of colonies, being made. After 10th June only two further collections were made, on 4th and 22nd July respectively.

The colonies were collected in different parts of the principal moat (Western Moat, Middle Moat, and Fungia Moat), but no differences in production were observed as between these different localities, which are nothing more than the parts of a very large pool. The

colonies were usually brought to the island in buckets, each bucket containing on an average 20 to 30 of them. The planulae were subsequently picked out and counted. Sometimes colonies were then isolated from one another, by putting each into a finger-bowl of clean sea-water and allowing them to stand overnight; so that the relative numbers of planulae which they were producing could be observed. In such cases it would usually be found that one or two of them would produce planulae in considerable numbers (100 or more), the remainder each liberating only 2 or 3, or a small number. The greatest number of planulae was always obtained from the water in which the corals were collected, suggesting that the disturbance due to their removal from the reef acted as a stimulus to the liberation of larvae.

The numbers of planulae counted on the various dates are represented graphically in Text-fig. 6, and listed in full in the table on p. 242. From these it will be seen that production remained fairly high from 26th January until 10th June; and that at the two July collections it was much lower. Even in June the maximum number of planulae was lower than previously. No collection made during the entire period produced a negative result, and until July the number of planulae obtained from one pail on any one day never fell as low as a hundred and rarely below five hundred.

From these data it is quite evident that massive *Porites* was actively breeding on the Low Isles reef during the period January to May, 1929; and that the production was apparently falling off during June and July. If we are right in concluding that all the planulae belong to one species, then there is no suggestion of lunar periodicity in this breeding season, which would appear to be a continuous one.

POCILLOPORA BULBOSA.

In the case of this coral all the planulae certainly belonged to a single species.

The corals were collected, as in the case of *Porites*, in the several parts of the principal moat. The species is a branched one, and during each collection branches were broken from a number of colonies. Sometimes the branches from each colony were brought to the island in separate jars, and subsequently isolated in finger-bowls; in other cases they were brought in buckets, in which case branches from different colonies were mixed. When the samples were isolated it was sometimes found that all of them produced planulae; sometimes that none of them did so; and at other times that some did so and others did not. In certain instances a collection from one part of the moat would produce a different result from a collection made on the same day in another part. The number of collections made altogether was in the neighbourhood of 80, and represented hundreds of colonies. The planulae, as before, were counted.

It may be noted that the collection of branches seems to be a better way of obtaining planulae than the taking of tow-nettings close to the coral. A tow-netting taken on a day when *Pocillopora* was known to be fertile, right round the moat and only about a foot above the coral, produced no planulae at all; and in the regular tow-nettings taken by Russell and Colman planulae were never captured over the reef flat, and but rarely out at sea.

The record begins with 7 collections which were made from 24th August to 5th September, 1928. No planulae were liberated from any of the samples then obtained,

with the exception of about 20 which were produced on 30th to 31st August. Full moon was on the 31st.

After this we have only two records before December. On 16th September and 4th November no planulae were produced from our samples.

From 11th December, 1928, to 24th July, 1929, the record is fairly continuous. The longest gap between collections, during that time, was 16 days, and was usually much less, the collections sometimes covering several consecutive days.

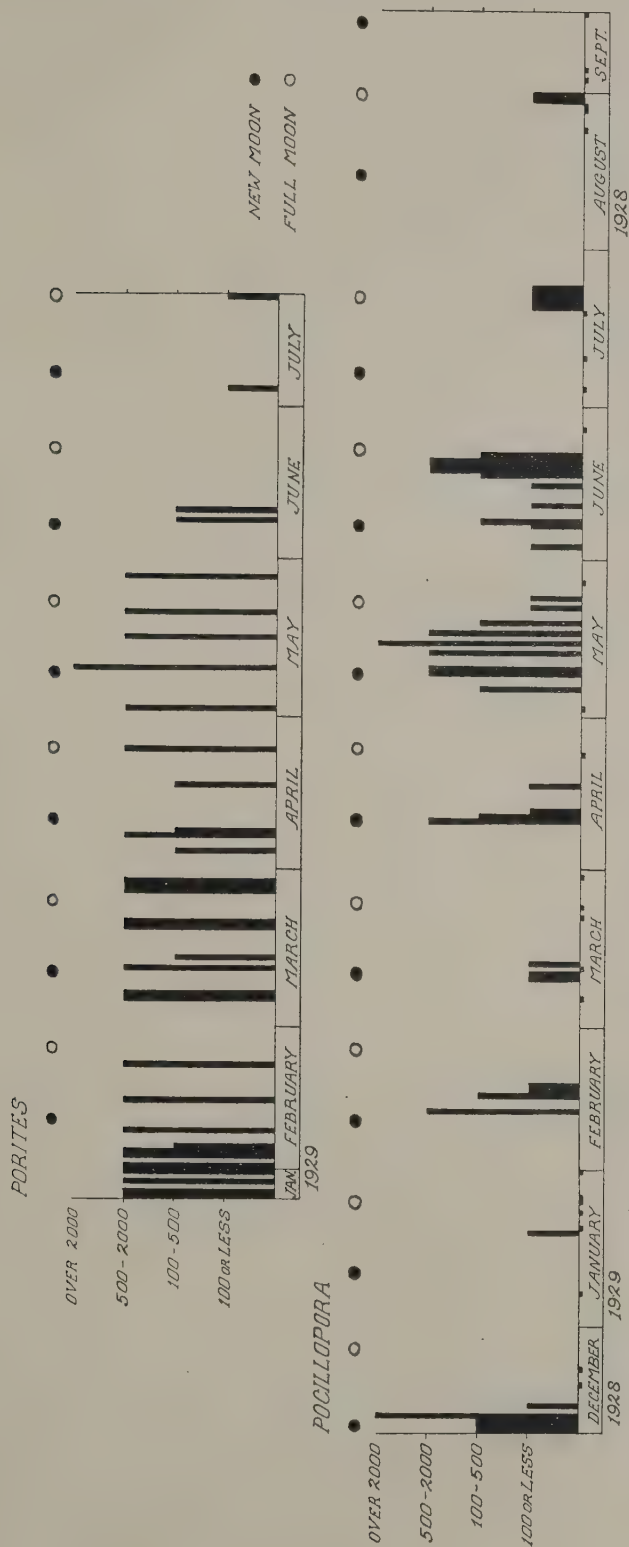
The results of this work are represented graphically in Text-fig. 6, and listed in detail in the table on p. 243. From the figure it may be seen that—

(1) Planulae were not obtained at every collection, as in the case of *Porites*. As will appear later, the negative results in this instance are as important as the positive ones.

(2) Planulae were obtained at about the time of new moon in the months December, February, March and April. The number obtained over each of these periods was large (1500 upwards), except in March, when less than 100 were counted. Between each of these four spawning-periods there were periods during which collections produced no planulae at all. In other words, there is evidence here of discontinuous breeding, the breeding periods occurring at about the time of *new moon* in each of the months mentioned. There is, however, a gap in January, which we cannot adequately fill. We know that after the December breeding period, and again in the latter part of January, negative results were obtained from collections, and also that somewhat *after* the time of new moon in January a few planulae were obtained; but we were prevented from collecting at the time of the new moon itself, and cannot, therefore, certify a breeding season at that time. It is probable, however, that the few planulae collected on 19th January represented the tail end of such a period.

(3) In the months of July, 1929, and August, 1928, planulae were obtained at about the time of *full moon*. The numbers collected were quite small. Negative collections were made before and after the productive period in August, and before the productive period in July; and collections at about the time of new moon in July produced no planulae.

From the above data we think it fair to conclude that in all probability *Pocillopora bulbosa* breeds discontinuously; that during the months December to April (summer and the beginning of winter), its breeding periods occur at about the time of new moon; and that during the months July and August (winter) they occur at about the time of full moon. If this is the case, we should expect a transitional period between the two phases. Such a transition is actually demonstrable between the last of the new-moon breeding periods (April) and the first full-moon period (July). Breeding occurred at and for some time *after* new moon in May, and for some time *before* full moon in June; during the interval between these two periods, it died down less completely than usual, but the definitive breeding period in June was delayed almost until full moon. In fact, it is possible that breeding was actually continuous, even though less active, during this interval, since we have only one negative record between the May and June breeding peaks, occurring among collections which yielded planulae in small numbers. The collections were neither frequent enough nor large enough to make it possible to rely too much on a single negative result. It may also be noted that the peak of production in June was less high than in May. The period of the opposite transition, from full moon to new, would occur some time between August and December; but our records do not cover that period.



TEXT-FIG. 6.—*Porites haddoni* and *Pocillopora bulbosa*. Diagrams representing the numbers of planulae obtained from these two species on various dates. For further comments see the text, p. 238. In this figure the number of planulae given for any one date is the number calculated as being derived from one pailful of samples. For purposes of calculation one pailful is taken as the equivalent of 24 samples. In the case of *Pocillopora*, the small rectangles below the line indicate negative records.

In Table I an attempt has been made to summarize the results of the collections in another way. For the purposes of this table each lunar month has been divided into eight approximately equal periods, the centre of each period corresponding to a phase of the moon (new moon, first quarter, etc., and the intermediate points). Opposite each such period is listed the number of collections made during that period; and the collections are recorded simply as positive (planulae produced) or negative (no planulae produced). The year is divided into three parts according to the type of production taking place, and the data for the several months included in any one of these parts are added together. This table emphasizes the fact that from December to April production took place only at or soon after new moon, while from July to November it took place only at and just after full moon. In May and June, the transition months, planula production was almost continuous, the only blank periods occurring soon after full moon.

TABLE I.—*Summary of data for Pocillopora bulbosa.*

Moon.	December to April.		May and June.		July to November.	
	+	—	+	—	+	—
●	7	1	4	0	0	0
◐	6	0	2	0	0	2
◑	4	2	3	0	0	1
○	0	3	4	0	0	3
◌	0	4	4	0	6	0
◍	0	1	0	2	1	2
◎	0	1	0	1	0	1
●	0	2	2	0	0	1

If our conclusion is justified, we have here an example of lunar periodicity of a novel description. Cases are already on record, and their number is steadily increasing, of animals which breed in relation to some definite phase of the moon; but so far as we are aware this is the first example of a transition from one phase of the moon to another phase, at a different time of year. We are aware that our data are, by force of circumstances, less complete than is to be desired; but feel that at present they are open to no other interpretation than the one made.

Is there any explanation which will help to elucidate a transition of this nature? So far as we can see at present there is none. There is a coincidence between the occurrence in question and the state of the tides, since during the summer months the lowest ebbs occur at the time of *full moon* and *at night*, whereas during the winter (May to October) they occur at the time of *new moon* and *in daytime*; but whether there is any connection between the tidal cycle and the reproductive cycle of the coral it is impossible to tell.

The whole question of the relationship of daylight, moonlight and other factors to the question of reproductive maturity is one which at present is developing rapidly, but which we do not propose to discuss at the moment.

4. SUMMARY.

1. The corals studied were *Montipora ramosa*, *Acropora hebes*, *Psammocora gonagra*, *Pocillopora bulbosa*, *Porites haddoni*, *Favia* (*Goniastrea*) *pectinata*, *Favia doreyensis*, *Symphyllia recta*, *Pavona cactus* and species of *Lobophyllia*.

2. The position and structure of the gonads is described in the cases of *Favia doreyensis*, *Symphyllia recta* and species of *Lobophyllia*, from both living and preserved material. *Favia doreyensis* is hermaphrodite; the same applies to at least one species of *Lobophyllia*, and probably also to *Symphyllia recta*.

3. In *Favia doreyensis* the ova and testes occur, intermingled, on the same mesentery. The mature eggs are large (305–374 μ in diameter), and occupy a considerable amount of space in the body of a fertile polyp (Text-fig. 2). The gonads are reduced to a more or less completely rudimentary condition during the non-breeding season, becoming bulky as they mature. The development of the testes seems to lag somewhat behind that of the ova as the gonad matures, but probably both eggs and sperms become ripe at about the same time. Apparently the colonies of this species first become strongly fertile, on the average, when their diameter reaches a figure in the neighbourhood of 10 cm.

4. From periodic examinations of the state of the gonads, it is concluded that the majority of colonies of *Favia doreyensis* spawn in early summer (December), after which the gonads become rudimentary and remain so for some months, beginning to mature again some time in June. The act of spawning, however, was not witnessed. In the cases of *Symphyllia* and *Lobophyllia* no definite conclusion can be drawn from the data obtained; but it is possible that they may have spawning periods close to that of *Favia doreyensis*.

5. A colony of *Pavona cactus* spawned in the Western Moat on 30th November, 1928, liberating clouds of sperms. Seven polyps belonging to this colony were sectioned; they were all male, and their condition is described on pp. 234–5.

6. The liberation of planulae was studied in *Montipora ramosa*, *Acropora hebes*, *Psammocora gonagra*, *Pocillopora bulbosa*, *Porites haddoni*, and *Favia pectinata*. Of these species, only *Pocillopora* and *Porites* produced any planulae whilst under observation, the details being as follows:

7. In massive *Porites* (the data probably all apply to *P. haddoni*) breeding was going on actively from January to May, 1929. It still continued during June and July, but less actively. There is no indication of lunar periodicity in this coral.

8. In the case of *Pocillopora bulbosa*, evidence is presented which appears to warrant the conclusion that this species breeds discontinuously; that its breeding seasons occur about the time of new moon in the months December to April (summer and early winter); but that during the months July and August (winter) they occur at about the time of full

moon. There is a transition period in May-June. This appears to be the first case on record of a transition in spawning from new moon at one time of year to full moon at another.

9. Among the corals studied, therefore, we have one case (*Favia doreyensis*) of a short breeding-season in early summer; another (*Porites haddoni*) of a long continuous season lasting from summer into winter; and a third (*Pocillopora bulbosa*) of discontinuous breeding continued over most (if not the whole) of the year, and exhibiting distinct lunar periodicity.

5. TABLES.

In the following tables the word "sample" usually means a *whole colony* in the case of *Porites*, a *group of branches* taken from a single colony in the case of *Pocillopora*. The number of planulae given in the last column represents the total number liberated by the material collected on the date opposite which the number is recorded. Actually, in the case of certain of these records, some of the planulae would be given off on the day of collection, others during the subsequent night and morning, or occasionally even later. In column 2 the letters used indicate the part of the principal moat from which the material came; F = Fungia Moat, Ma = Madrepora Moat, M = Middle Moat, W = Western Moat; B refers to the part of the moat opposite a low place in the rampart, at the junction of the Fungia and Madrepora Moats.

TABLE II.—*Production of planulae by Porites haddoni.*

Date	Locality	Amount collected	Number of colonies which produced planulae.	Number of planulae produced	Date	Locality	Amount collected	Number of colonies which produced planulae.	Number of planulae produced.
1929.					1929.				
Jan. 26	W	1 pail		1100	Mar. 21	M, W	3 pails		3600
" 26	F	ca. 9 samples		A few	" 27	W	2 "		ca. 1200
" 26		1 colony		Dozens	" 28	M	3 "		2200
" 27	W	69 samples		ca. 2000	" 29	M	3 "		1600
" 27	W, M			Hundreds	April 4	W, M	4 "		1150
" 29		1 pail ?		1600	" 7	F, M	3 "		2500
" 31				A good crop	" 8	M	4 "		1700
Feb. 1		2 pails		1200	" 17	F	1 pail		119
" 3		2 "		1200 +	" 24	W, M	16 colonies.	14	83
" 4	M	2 " ?		4000	" 24	W, M	10 "		780
" 5	W	29 samples	Many	500 +	May 2	M, W	22 "		1100
" 8	M			Large number	" 10	F	12 "	12	2500-3000
" 14	M			Many	" 16	M	15 "		600-700
" 21		3 pails ?		5000	" 21	M, F	2 pails		1700
Mar. 6	W	12 colonies		800-900	" 28	F	2 "		ca. 2000
" 7	W	3 pails		3400	June 8	M	12 colonies	9	250
" 12	M	3 "		2100	" 10	F, M	6 pails		1050
" 14	M	3 "		1000	July 4	F, M	$\frac{1}{2}$ pail		26
" 20	M, W	2 "		1350	" 22		$\frac{1}{2}$ "		17

TABLE III.—*Production of planulae by Pocillopora bulbosa.*

Date.	Locality.	Amount collected.	Number of colonies which produced planulae.	Number of planulae produced.	Date.	Locality.	Amount collected.	Number of colonies which produced planulae.	Number of planulae produced.
1928.					1929.				
Aug. 24	W	12 samples		0	Mar. 24	Ma	12 samples		0
" 28	W	ca. 3 samples		0	" 30	Ma	1 pail		0
	(probably)				April 10	F	1 "		1450
" 29	W			0	" 11	F	2 pails		1361
" 30	W	6 samples		ca. 18	" 11	Ma	2 "		535
" 31	W	6 "		2	" 11	Ma, B	12 samples	7	69
	(probably)				" 12	W	1 pail		24
Sept. 3	W	6 "		0	" 17	F	1 "		8
" 5	W	6 "		0	" 23	F	12 samples		0
" 16	F	6 "		0	May 2	F	14 "		0
Nov. 4	W	12 samples		0	" 6	F	1 pail		150-200
Dec. 11	W	12 "	At least 8	ca. 123	" 9	Ma, F	1 "		1000
" 12	W	12 "	At least 8	ca. 110	" 9	Ma	12 samples	12	340
" 13	F	12 "		70 at least	" 10	B	3 pails		5000
" 14	Ma	24 "		2549 + many not counted	" 13	B	$\frac{1}{2}$ pail		1000
" 16				24	" 15	B	$\frac{1}{2}$ "		2000
" 20				0	" 17	B	$\frac{1}{2}$ "		550
" 23	Ma	25 samples		0	" 19	F, B	$\frac{1}{2}$ "		75
1929.					" 22	Ma, B	12 samples	2	6
Jan. 7	Ma	12 "		0	" 24	B	$\frac{1}{2}$ pail		17
" 19				15	" 27	B	$\frac{1}{2}$ "		0
" 20				0	June 3	B	$\frac{1}{2}$ "	1	1
" 23				0	" 7	Ma, B	3 pails		30
" 25				0	" 7	Ma	12 samples	3	5
" 26				0	" 8	M	$\frac{1}{2}$ pail		52
" 31		1 collection		0	" 11	B	$\frac{1}{2}$ "		25
Feb. 12	Ma	12 samples	12	Hundreds probably over 1000	" 15	M, Ma	$\frac{1}{2}$ "		26
" 15		1 pail		Hundreds	" 17	M, B	$\frac{1}{2}$ "		128
" 16				Few	" 18	M, B	1 "		830
" 17		1 pail		Very few	" 19		12 samples	4	6
Mar. 6	W	12 samples		0	" 19	M	$\frac{2}{3}$ pail		525
" 10	F	1 pail		27	" 20		12 samples	ca. 7	Numerous
" 11	W, M	1 "		0	" 20	M, B	8 pails		> 4000
" 11	F	1 "		47	" 21		9 samples	6	Numerous
" 12	Ma	12 samples		0	" 26	F	$\frac{1}{2}$ pail		0
" 13	F	1 pail		2	July 4	F, M	$\frac{1}{2}$ "		0
" 22	F	1 "		0	" 10	M	1 "		0
					" 19	B	1 "		0
					" 20		1 "		2
					" 21		1 "		1
					" 22		$\frac{3}{4}$ "		54
					" 23	M, W, B	6 pails		28
					" 24		2 "		21

6. REFERENCES.

1. CORAL GONADS.

The following list includes only a selection of leading citations; from the works mentioned further references may be obtained.

- BOURNE, G. C. 1888. On the Anatomy of *Mussa* and *Euphyllia*, and the Morphology of the Madreporarian Skeleton. Quart. J. Micr. Sci., London, XXVIII, pp. 21-51, 2 pls.
- 1905. Report on the Solitary Corals Collected by Prof. Herdman, at Ceylon, in 1902. Ceylon Pearl Oyster Fisheries, London, Supplementary Report, No. 29, pp. 187-242, 4 pls., text-illust.
- DUERDEN, J. E. 1902. West Indian Madreporarian Polyps. Mem. Nat. Acad. Sci., Washington, VIII, pp. 401-597, 25 pls.; text-illust.
- FOWLER, G. H. 1885. The Anatomy of the Madreporaria: I (*Flabellum* and *Rhodopsammia*). Quart. J. Micr. Sci., London, XXV, pp. 577-597, 3 pls.

- FOWLER, G. H. 1887. The Anatomy of the Madreporaria: II (*Madrepora*). Quart. J. Micr. Sci., London, XXVII, pp. 1-16, 1 pl.
- 1888. The Anatomy of the Madreporaria: III (*Turbinaria*, *Lophohelia*, *Seriatopora*, *Pocillopora*). Quart. J. Micr. Sci., London, XXVIII, pp. 1-19, 2 pls.
- 1888. The Anatomy of the Madreporaria: IV (*Madracis*, *Amphihelia*, *Stephanophyllia*, *Sphenotrochus*, *Stephanaria*, *Pocillopora*, *Seriatopora*). Quart. J. Micr. Sci., London, XXVIII, pp. 413-430, 2 pls.
- 1890. The Anatomy of the Madreporaria: V (*Duncania*, *Madrepora*, *Galaxea*, *Heteropsammia*, *Bathyactis*). Quart. J. Micr. Sci., London, XXX, pp. 405-419, 1 pl., text-illust.
- GARDINER, J. S. 1900. On the Anatomy of a Supposed New Species of *Coenopsammia* from Lifu. Willey's Zoological Results, Cambridge, part 4, pp. 357-380, 1 pl., text-illust.
- 1902. Some Notes on Variation and Protandry in *Flabellum rubrum*, and Senescence in the Same and Other Corals. Proc. Cambridge Philos. Soc. XI, part 6, pp. 463-471.
- 1904. South African Corals of the Genus *Flabellum*, with an Account of their Anatomy and Development. Marine Investigations in South Africa, Cape of Good Hope Dept. of Agriculture, Cape Town, II, pp. 117-154, 4 pls., text-illust.
- 1904. The Turbinolid Corals of South Africa, with Notes on their Anatomy and Variation. Marine Investigations in South Africa, Cape of Good Hope Dept. of Agriculture, Cape Town, III, pp. 95-129, 3 pls.
- LACAZE-DUTHIERS, H. DE. 1897. Faune du Golfe du Lion: Coralliaires. Zoanthaires sclérodermes. Arch. Zool. Expér. Gén., Paris, ser. 3, V, pp. 1-249, 12 pls., text-illust.
- MATTHAI, G. 1914. A Revision of the Recent Colonial Astreaeidae Possessing Distinct Corallites. Trans. Linn. Soc., Zool., London, XVII, pp. 1-140, 38 pls.
- 1919. On *Favia conferta*, Verrill, with Notes on other Atlantic Species of *Favia*. Brit. Mus. (Nat. Hist.), Brit. Antarctic ("Terra Nova") Exped., 1910, Nat. Hist. Reports, Zool., London, V, No. 2, pp. 69-96, 4 pls., text-illust.
- 1928. A Monograph of the Recent Meandroid Astreaeidae. Catalogue of the Madreporarian Corals in the British Museum (Nat. Hist.), London, VII, pp. 325, 72 pls., text-illust.
- MOSELEY, H. N. 1881. On Deep-sea Madreporaria. "Challenger" Reports, Zool., London, II, pp. 127-248, 16 pls., text-illust.
- PRATT, E. M. 1900. Anatomy of *Neohelia porcellana* (Moseley). Willey's Zoological Results, Cambridge, part 5, pp. 591-602, 2 pls.

2. LUNAR PERIODICITY.

For references previous to 1928 see the papers of Amirthalingam and Herpin; further references since 1928 may be obtained from the works cited.

- AMIRTHALINGAM, C. 1928. On Lunar Periodicity in Reproduction of *Pecten opercularis* near Plymouth in 1927-8. J. Mar. Biol. Ass. U.K., Plymouth, XV, pp. 605-641, text-illust.
- ARMSTRONG, H. E. 1932. Light and Sexual Periodicity. Nature, London, CXXIX, p. 906.
- BAKER, J. R., and RANSON, R. M. 1932. Factors Affecting the Breeding of the Field Mouse (*Microtus agrestis*). Part I: Light. Proc. Roy. Soc., London, B, CX, pp. 313-322, text-illust.
- BISSENETTE, T. H. 1930. Studies on the Sexual Cycle in Birds. I: Sexual Maturity, its Modification and Possible Control in the European Starling (*Sturnus vulgaris*). Amer. J. Anat., Philadelphia, XLV, pp. 289-305, 2 pls.
- 1930. Studies on the Sexual Cycle in Birds. III: The Normal Regressive Changes in the Testis of the European Starling (*Sturnus vulgaris*) from May to November. Amer. J. Anat., Philadelphia, XLVI, pp. 477-497, 2 pls.
- 1930. Studies on the Sexual Cycle in Birds. IV: Experimental Modification of the Sexual Cycle in Males of the European Starling (*Sturnus vulgaris*) by Changes in the Daily Period of Illumination and of Muscular Work. J. Exp. Zool., Philadelphia, LVIII, pp. 281-319, 3 pls.
- 1931. Studies on the Sexual Cycle in Birds. V: Effects of Light of Different Intensities upon the Testis Activity of the European Starling (*Sturnus vulgaris*). Physiol. Zool., Chicago, IV, pp. 542-574, 3 pls.
- 1932. Studies on the Sexual Cycle in Birds. VI: Effects of White, Green, and Red Lights of Equal Luminous Intensity on the Testis Activity of the European Starling (*Sturnus vulgaris*). Physiol. Zool., Chicago, V, pp. 92-123, 4 pls.
- 1932. Light and Diet as Factors in Relation to Sexual Periodicity. Nature, London, CXXIX, p. 612.

- BISSONNETTE, T. H., and CHAPNICK, M. H. 1930. Studies on the Sexual Cycle in Birds. II: The Normal Progressive Changes in the Testis from November to May in the European Starling (*Sturnus vulgaris*), an Introduced, Non-migratory Bird. Amer. J. Anat., Philadelphia, XLV, pp. 307-343, 7 pls.
- and WADLUND, A. P. R. 1931. Spermatogenesis in *Sturnus vulgaris*: Refractory Period and Acceleration in Relation to Wave-length and Rate of Increase of Light Ration. J. Morph., Philadelphia, LII, pp. 403-427, 3 pls.
- BRAMSON, J. 1929. Statistisch onderzoek naar de correlatie tusschen maanphase en menstruatie bij 10,000 vrouwen. Psychiatr. en Neurol. Bladen, Amsterdam, XXXIII, I, pp. 63-76, 4 figs.
- CUNNINGHAM, J. T. 1932. Light as a Factor in Sexual Periodicity. Nature, London, CXXIX, pp. 543-4.
- FOX, H. M. 1932. Lunar Periodicity in Reproduction. Nature, London, CXXX, p. 23.
- HERPIN, R. 1928. Étude sur les essaimages des Annélides polychètes. Bull. Biol. France Belgique, Paris, LXII, pp. 308-377, text-illustr.
- 1929. Étude sur les essaimages des Annélides polychètes (note complémentaire). Bull. Biol. France Belgique, Paris, LXIII, pp. 85-94.
- JUST, E. E. 1929. Breeding Habits of *Nereis dumerilii* at Naples. Biol. Bull., Woods Hole, LVII, pp. 307-310.
- LLEWELLYN, LL. J. 1932. Light and Sexual Periodicity. Nature, London, CXXIX, p. 868.
- MARRIAN, G. F., and PARKES, A. S. 1929. The Effect of Anterior Pituitary Preparations Administered during Dietary Anoestrus. Proc. Roy. Soc., London, B, CV, pp. 248-258, 2 pls., text-illustr.
- MARSHALL, F. H. A. 1932. Light as a Factor in Sexual Periodicity. Nature, London, CXXIX, pp. 344 and 361.
- MOORE, C. R., and SAMUELS, L. T. 1931. The Action of Testis Hormone in Correcting Changes Induced in the Rat Prostate and Seminal Vesicles by Vitamine B Deficiency or Partial Inanition. Amer. J. Physiol., Baltimore, XCVI, pp. 278-288, 1 pl.
- PHILIP, G. 1932. Light as a Factor in Sexual Periodicity. Nature, London, CXXIX, p. 655.
- RAMANATHAN, O. 1932. Light and Sexual Periodicity in Indian Buffaloes. Nature, London, CXXX, pp. 169-70.
- RANZI, S. 1931. Ricerche sulla Biologia Sessuale degli Anellidi. Pub. Stat. Zool. Napoli, XI, fasc. 2, pp. 271-292, diagrams.
- ROWAN, W. 1928. Reproductive Rhythm in Birds. Nature, London, CXXII, pp. 11-12, text-illustr.
- RUSSELL, F. S. 1932. Behaviour in Invertebrates. Nature, London, CXXIX, p. 473.
- SEMMENS, E. S. 1932. Hydrolysis in Green Plants by Moonlight. Nature, London, CXXX, p. 243, text-illustr.
- SHULL, A. F. 1929. Determination of Types of Individuals in Aphids, Rotifers and Cladocera. Biol. Reviews, Cambridge, IV, pp. 218-248.
- 1930. Control of Gamic and Parthogenetic Reproduction in Winged Aphids by Temperature and Light. Zeitschr. Indukt. Abstamm.-u. Vererbungsl., Leipzig, LV, pp. 108-126.
- TATE, P., and VINCENT, M. 1932. Influence of Light on the Gorging of *Culex pipiens* L. Nature, London, CXXX, pp. 366-7.
- TINKER, M. A. H. 1932. Light as a Factor in Sexual Periodicity. Nature, London, CXXIX, p. 543.

DESCRIPTION OF PLATE I.

(For more detailed descriptions of these figures, see the text, pp. 222-3.)

FIG. 1.—*Euphyllia glabrescens*. A group of branches broken away from a hemispherical colony. Photographed during life, with the polyps half expanded. Slightly larger than natural size.

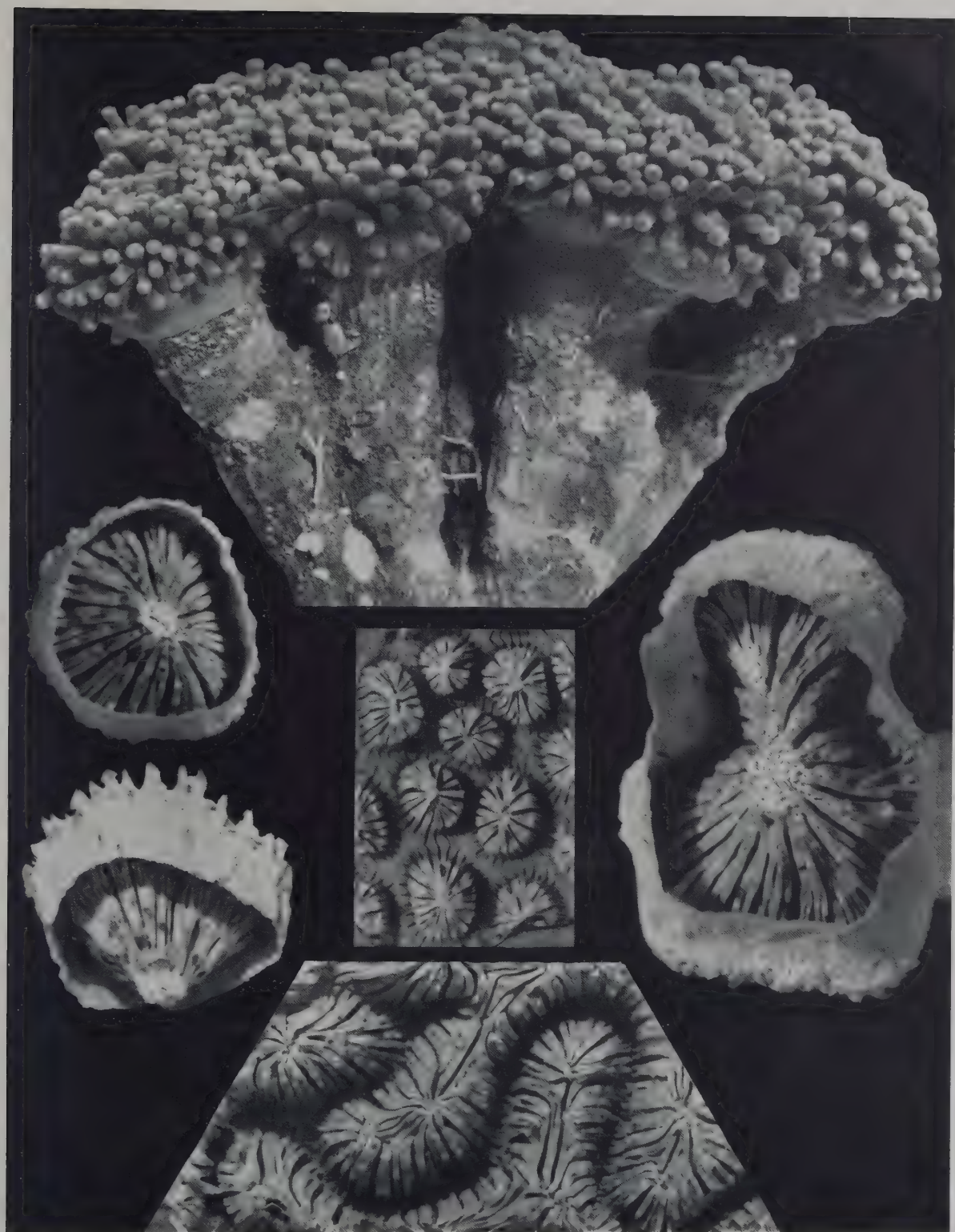
FIGS. 2 and 3.—*Lobophyllia corymbosa*. Two views of a contracted, decalcified polyp; seen from below in fig. 2, more from the side in fig. 3. Fig. 2 $\times 1.7$; fig. 3 $\times 1.8$.

FIG. 4.—*Lobophyllia* sp. A single contracted, decalcified polyp, viewed from below. $\times 1.8$.

FIG. 5.—*Symphyllia recta*. Part of the central portion of a colony, decalcified and viewed from below. $\times 1.7$.

FIG. 6.—*Favia doreyensis*. Part of the central portion of a colony, decalcified and viewed from below. $\times 1.6$.

The material photographed for this Plate was collected at Low Isles, with the exception of the specimen represented in fig. 1, which came from Batt Reef.



THE BREEDING OF REEF ANIMALS

PART II. INVERTEBRATES OTHER THAN CORALS

BY

ANNE STEPHENSON,

Department of Zoology, University of Cape Town

WITH FOURTEEN TEXT-FIGURES AND FOUR TABLES

CONTENTS.

	PAGE
PREFACE	247
A NOTE ON THE NUMBER OF ANIMALS USED	248
DESCRIPTION OF THE RESULTS	249
SPAWN COLLECTED ON THE REEF	266
SUMMARY AND CONCLUSIONS	266
REFERENCES	272

PREFACE.

THE description of the breeding of corals, by Sheina M. Marshall and T. A. Stephenson, is published in Vol. III, No. 8 of these reports. The present work, on the breeding of invertebrates other than corals, was carried out by the author, with the assistance, during the latter part of the period, of E. A. Fraser, who took over the investigations of *Cypræa annulus* from 13th March to 15th June, 1929, and of *Myrionema amboinense* from 11th March onwards; and of S. M. Manton, who worked on *Thalamita stimpsoni* from 2nd April to 15th June, 1929, and on *Centrechinus setosus* from 2nd April to 14th June, 1929. Dr. Fraser has published an account of *Myrionema amboinense* in report No. 4 of this volume. Other members of the expedition also constantly helped throughout the year in the collection of both material and spawn. To all of them I extend my most hearty thanks; and also to T. A. Stephenson for guidance in the preparation of the report.

When selecting the animals on which to carry out the research, the aim was to choose representatives of the main invertebrate groups, with special reference to those which were most important on the reef. Unfortunately various circumstances considerably hampered the choice. For instance, the gastropod *Pterocera* and the star-fish *Linkia*, which would otherwise have been suitable, were so difficult to open up for the weekly examination of the gonads that it proved impracticable to use them. No worm or sponge

could be found which was both suitable and sufficiently plentiful; and prawns, though not uncommon, were difficult to secure. In arranging for a long period of weekly routine work on living animals, the tides played a very important part; during neaps certain animals would have been unavailable for long periods, and it was impossible to keep them artificially in the perfect condition which is essential for work on breeding.

The animals finally chosen were :

COELENTERATA.

Myrionema amboinense.

ECHINODERMATA.

Ophiothrix longipeda.

Tripneustes gratilla.

*Centrechinus (Diadema) setosus.**

MOLLUSCA.

*Acanthozostera gemmata.**

Cypræa annulus.

*Hippopus hippopus.**

CRUSTACEA.

Thalamita stimpsoni.

In addition to this, work was done by other members of the expedition on the breeding of the following animals :

Trochus niloticus. See F. W. Moorhouse, 1932.

Pinctada margaritifera. See A. G. Nicholls, 1931.

F. W. Moorhouse also worked on the gonads of several species of Bêche-de-Mer and of oysters, but his results are not yet available.

A NOTE ON THE NUMBER OF ANIMALS USED.

The numbers used in this paper are low (3655 animals were involved), which fact is due to several causes. It must be borne in mind that the reef itself was small, its major axis being only about one mile; the number of animals, therefore, of a large enough size for use in this investigation was not so great that there was an unlimited supply available for a year's work. This was particularly noteworthy in the case of *Tripneustes* and *Centrechinus*, the supply of which was running out by the end of the year. Then the animals which lived on the *Thalamita* flat,† *Ophiothrix* and *Thalamita*, were by no means unduly plentiful, and were not easy to catch. The supply of these two species and of *Acanthozostera* became very difficult during the period of bad day-tides in the summer. In addition to these restrictions, only a certain amount of time could be allowed for this work; the collection and examination of specimens, and the execution of experiments, is in any case a considerable undertaking.

Although, had it been possible, it would have been preferable to employ larger numbers, it is felt that too much stress can be laid on the necessity for large numbers in work of this description. The numbers actually used have, in fact, produced such consistent results that it is doubtful whether larger numbers would have affected the

* Animals marked with an asterisk are illustrated in Vol. III, No. 2 of these reports, Pls. XVIII, XX and XXI.

† For all references to habitats in this paper see Vol. III, No. 2, Text-fig. 2, of these reports.

conclusions apart from giving them a greater degree of precision. It may be noted in favour of these particular investigations that they deal with continuous observations for eleven months on animals living in a very restricted area. Further, the specimens used for any one species were collected as far as possible from a single habitat on the reef, and therefore belonged to a community subjected to no changes other than the ordinary seasonal ones.

DESCRIPTION OF THE RESULTS.

Myrionema amboinense.

Number of colonies examined, 478.

Weekly examination of 12 colonies, 11th August, 1928 to 3rd January, 1929; 29th January, 1929 to 15th June, 1929.

Average height of colonies, 1.5 cm.

Range of size, 0.7–3.8 cm.

In every month of the year, and in each week of each month (with three exceptions), some of the colonies examined bore definite gonophores. The proportion of fertile colonies varied from one month to another, but this variation means very little, since at first healthy-looking colonies were collected in preference to apparently poorly developed ones; but it was found later on that female gonophores occurred more commonly on colonies which had lost many of their polyps, and which therefore appeared less robust. It is clear, however, that from August 1928 to June 1929 some colonies of *Myrionema* were in a fertile condition. Whether the development of planulae occurred in all these months cannot be stated, but from Dr. Fraser's work in the months March to June, 1929, we know that planulae were being formed in March, April, May and June. An account of the details of development in this species has already been published by Dr. Fraser in Vol. III, No. 4 of these reports.

Ophiothrix longipeda.

Number of specimens examined, 388 (172♂, 180♀, 36 indeterminate).

Weekly examination of 12 specimens, 16th August, 1928 to 5th January, 1929; 30th January, 1929 to 25th April, 1929.

Further examinations 22nd and 29th May, 15th June, 1929.

Average diameter of disc 2.2 cm.

Range of size, 1.2–3.7 cm.

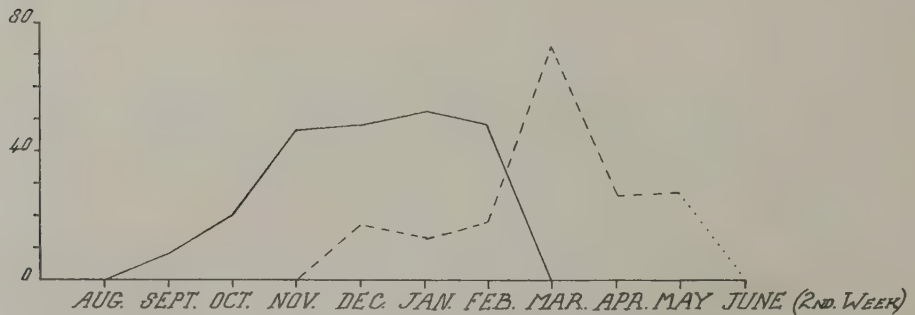
Ophiothrix longipeda was common on various parts of the reef; the collections were all made from under boulders on the Thalamita flat. The species is a large one, with a span of 2 ft. or more in full-grown specimens.

THE MALE GONAD.—When the animal was immature the testes were only visible as small white patches on the gut diverticula, and were often difficult to find; but when mature they were thick, spread well over the diverticula, and were a deep cream in colour, discharging a plentiful milky flow containing active sperms when cut. The sperms, when examined microscopically, never showed the intense activity of those of other animals examined, and their movements very rapidly subsided. Shortly after spawning had occurred the testes became small and collapsed.

THE FEMALE GONAD.—In the female the immature ovary was a brownish pink in colour, which changed to a dull but deep pink when the animal matured. The gonad then



TEXT-FIG. 1.—*Ophiothrix longipeda*. Section of part of a ripe ovary. The nuclei are mostly in synizesis.



TEXT-FIG. 2.—*Ophiothrix longipeda*. Graphs showing the percentage of mature and spent gonads (♂ and ♀) for each month. Continuous line, mature and nearly mature specimens; broken line, spent and resting specimens; dotted line represents probability only, since there was only one examination in June. The maximum number of mature individuals was reached in the summer months, the peak number of spent individuals following closely afterwards.

became of a very fluid consistency and the eggs (Text-fig. 1) were coloured reddish brown. In the ovary of a female which had spawned, there were found mature, immature, and disintegrating eggs, suggesting that another spawning might occur later,

RESULTS OF ROUTINE WORK.—The examination of specimens in August 1928, showed that they were immature; in some cases it was difficult to determine the sex of the animal. By the end of September this difficulty had ceased, and a month later the definite activity of the sperms in the male, and the colour and other signs in the female, showed that the animals were maturing. By the end of November they seemed mature; the males contained numerous active sperms, and the females plentiful mature eggs, the gonads in both sexes being large and extensive. During December and January the gonads mostly seemed mature, and occasionally specimens appeared which seemed to be spent or partially so. In February spawning was actually observed in two cases; on the 6th one female shed its eggs during dissection; another spawned spontaneously in the aquarium on the night of the 11th. Towards the end of this month the gonads had diminished in size and the colour of the ovary was fading. This continued throughout March and into April, when many specimens could not be sexually determined at all. At the end of May there were signs of returning activity. Numerous immature eggs were then discovered, and a very slight flow began. In the batch examined in June (only one collection was possible) these signs were continued, but the animals were still far from mature.

CONCLUSION.—From these data it seems clear that the spawning of *Ophiothrix longipeda* occurred during the summer months, December to February; that there was only one spawning period in the year, followed by a resting stage in March and April; and that maturing began again from May onwards. These points are well brought out in the graphs reproduced in Text-fig. 2.

Tripneustes gratilla.

Number of specimens used, 581.

Number examined in routine work, 363 (158♂ and 205♀).

Number used for experiments in April, May and June, 1929, 218.

Weekly examinations of 6 or 12, 7th August, 1928 to 3rd January, 1929; 29th January, 1929 to 25th April, 1929.

Further examinations on 23rd and 28th May, and 15th June, 1929.

Average diameter of animal, 8.8 cm.

Range of size, 6.8–10.8 cm.

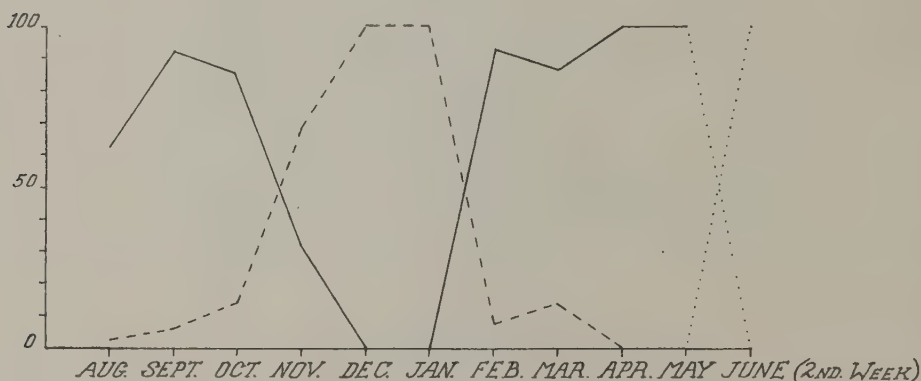
Of the two sea-urchins used in these experiments, *Tripneustes gratilla* gave the more satisfactory results. It was fairly common in certain parts of the reef, and was collected either from the Western Moat, or around the spit to which it gives its name. The species is a large Echinus-like form.

THE MALE GONAD.—When ripe the testes are large and plump, and usually cream in colour; cutting produces a plentiful milky flow of myriads of extremely active sperms. This activity dies down fairly soon after spawning, and a spent gonad gives practically no flow when cut, the whole organ having a peculiar granular watery appearance. In immature and spent specimens the gonad has often a greenish tinge, and is shrunken in size.

THE FEMALE GONAD.—This has the same granular appearance when spent as that of the male, and all flow ceases, thus making the judging of its condition fairly easy. The

immature ovary is of a dark greenish colour; on reaching maturity it is usually of a bright orange, and the yellow eggs pour out freely. The diameter of a ripe egg is about 90μ , and the nucleus is clearly visible.

RESULTS OF ROUTINE WORK.—When the observations were begun in August the specimens appeared to be maturing; in September and October most specimens seemed mature. By the end of November there was a marked change in the appearance of the gonad in both sexes. The gonads had a granular appearance, no flow occurred when they were cut, eggs were disintegrating, and sperms few and inactive. However, the gonads were still thick and extensive. By the end of January the specimens seemed to be maturing again, and during March, April and May the majority of them appeared to be mature. The one examination in June showed specimens with all the signs of being spent, with the additional one that the gonads had decreased in size and were small and inextensive.



TEXT-FIG. 3.—*Tripneustes gratilla*. Graphs showing the percentage of mature and spent gonads (♂ and ♀) for each month. Continuous line, mature and nearly mature specimens; broken line spent and resting specimens; dotted line represents probability only, since there was only one examination in June. The graphs indicate two periods of maturity with a quiescent period between.

FERTILIZATION EXPERIMENTS.—Attempts at artificial fertilization were frequently made during the weekly examinations, but apart from the fact that in reasonable circumstances (*i. e.* when the temperature was moderate), they agreed with the results obtained from the routine observations, they are not of any real value, as during the hot months the conditions made successful artificial fertilizations impossible. Three spawnings, however, were actually observed in the aquarium*; these occurred on the nights of 24th February, 24th April and 9th May, 1929.

A further series of experiments was carried out by S. M. Manton. Specimens were placed upside down on a board overnight, and a record made of the number which liberated eggs or sperm fluid under these conditions.† These experiments began on 24th April and ceased on 20th June, 1929; 218 animals were used and 95 spawned. Details are given in Table I.

* Specimens placed in the aquarium were treated beforehand as in the case of *Centrechinus*, p. 254.

† This method was employed by H. Munro Fox in studying the breeding of sea-urchins in the Red Sea (1924, p. 529).

CONCLUSION.—From a consideration of the results of the weekly observations, it would seem that in *Tripneustes gratilla* there are two resting and two active periods during the year. In the year in question the first activity occurred between September and November, followed in December and January by a more or less quiescent period; from March to May there was another burst of activity, which died down to another and more complete period of rest. This is expressed graphically in Text-fig. 3.

TABLE I.—*Experiments on Board.*

Date. 1929.	Number of animals used.	Number which spawned.	
		♂	♀
April 24	6	3	1
„ 25	6	2	1
„ 26	7	1	4
May 9	12	2	3
„ 10	8	4	
„ 11	12	6	1
„ 12	12	8	2
„ 13	12	3	2
„ 14	6	1	1
„ 15	6		
„ 17	12	5	1
„ 20	11	4	1
„ 22	12	4	
„ 24	12	6	1
„ 27	12	8	3
„ 29	12	4	3
„ 31	12	2	2
June 3	12	3	2
„ 14	12		
„ 17	12		
„ 20	12	1	
	218	67	28

Centrechinus setosus.

Number of specimens used, 429.

Number examined in routine work, 350 (157♀, 76♂, and 117 indeterminate).

Number used for experiments, 79.

Board experiments on 24th, 25th and 26th April, 9th and 10th May, 1929.

Aquarium observations on 26th December, 1928; 26th January, 23rd and 24th February, 25th March, 24th April, 9th and 10th May, 1929.

Weekly examinations of 6 or 12, 7th August to 31st December, 1928; 31st January to 29th May, 1929.

Further examination on June 14th, 1929.

Average diameter of animal, 6.4 cm. (spines not included).

Range of size, 3.0–8.4 cm.

The sea-urchin *Centrechinus setosus* was dealt with in exactly the same way as *Tripneustes gratilla*. It was fairly plentiful in some parts of the reef, and was collected from the North-East and Western Moats, and around *Tripneustes* Spit. Apart from the regular weekly examinations of gonads, a number of specimens were placed on a board upside

down, overnight, as in the case of *Tripneustes*, by S. M. Manton. Further, on several occasions specimens were put in a cage on the reef, in which they could not feed, for two nights and days, in order to get rid of their intestinal content; they were then transferred to the aquarium for observation, in the hope that they would spawn there.

THE GONADS.—During the whole experiment the gonads in both sexes, which varied in colour from cream to gold, were usually thick and extensive, with no marked variation in size throughout the year. In this animal the number of records of "sex indeterminable" is very high, and probably many of these cases may have been immature males. The females were easier to identify, although the ova were often very small and embedded in tissue.

RESULTS.—When the observations began in August 1928, a high percentage of specimens were difficult to determine as to sex, and the flow when the gonad was cut was either negligible or absent. The eggs, when present, were small and immature and deeply embedded in tissue. All these signs of immaturity slowly but definitely decreased as the year went on, and by November it was found that the sex of the animal could almost always be discovered easily. The flow in males was often plentiful and sometimes milky; myriads of active sperms were found; in females the eggs were larger, and freed themselves easily from the tissue. On 26th December, 1928, the only record of actual spawning was observed, when one specimen discharged a jet of sperm as it was being transferred from a collecting bucket into the aquarium. At about this time, also, isolated cases occurred of apparently spent or partially spent females, the gonads containing ova which seemed to be disintegrating. It was also noted that there seemed to be a slight fluctuation of ripeness in any one month, from August 1928 to March 1929. By March 1929, a definite decline in activity appeared to have set in, and in May as many as 50% of a batch of specimens would be indeterminable as to sex. Apart from the one case of spawning in the aquarium, neither keeping specimens in the aquarium nor inverting them on a board at night gave any positive result at all.

CONCLUSION.—Although the indications outlined above are somewhat unsatisfactory, they do point to a period of activity during the summer months, and to a quiescent period during the colder part of the year. It is curious that this species, in which Fox (1924) was able to demonstrate lunar periodicity in the Red Sea, should have given no certain sign of such periodicity at Low Isles. There is, however, no suggestion that periodicity was actually absent (note the fluctuation mentioned above within any single month); it might well have been possible to substantiate it with a fuller series of observations. In the Red Sea the species spawns for several months preceding and sometimes including September (*i. e.* in the warmer months as at Low Isles).

Acanthozostera gemmata.

Number of specimens used, 474.

Number examined in routine work, 335 (202♂ and 133♀).

Number used for experiments, 139.

Weekly examinations of 12, 6th August to 19th December, 1928; 28th January to 19th February, 1929.

Further examinations of 12 per month in March, April, May and June, 1929.

Average length of animal, 10.6 cm.

Range of size, 4.5–16.0 cm.

Acanthozostera gemmata is a chiton common on the reef, and has the advantage of growing to a large size—to a length of 14 cm. or more. The specimens used for dissection were collected on the Boulder Tract and on the beach Sandstone, C1. In the daytime the animal remains motionless in the crevices of the rocks and underneath and on the shady parts of boulders, but at night can be found creeping about with surprising speed over the exposed surfaces.

THE MALE GONAD.—The gonads were exposed by cutting off 4 or 5 of the 8 shell plates on the back with bone forceps. The colour of the male gonad is always red, but in immaturity it is of a dark shade, and when cut there is no flow, the gonad appearing a paler red inside; as the gonad ripens the colour gradually becomes much brighter, and there is an extensive milky flow which, when the testis is quite mature, gives it a whitish appearance.

THE FEMALE GONAD.—The female gonad in immaturity is a very dark reddish brown, which changes to a deep blue black when the eggs are mature. In this latter condition it is so fluid that it is difficult to handle at all. The ova are black, and develop rays before they are discharged from the ovaries (see Text-figs. 4 and 5). They are easily visible to the naked eye, and are about 120μ in diameter. When the female gonad is spent it has a mottled brown appearance and becomes far more solid. In Text-fig. 4 is shown a section through a nearly mature female gonad. It will be noticed that this contains eggs in several stages of maturity. In the lower part of the figure are quite unripe eggs with small nuclei and no rays, while above there are well-developed free eggs with large nuclei and many rays. Text-fig. 5 shows a living mature rayed egg, drawn from a specimen which spawned 29th September, 1928.

RESULTS OF ROUTINE WORK.—The condition of the specimens in the weekly examinations gave the following interesting results:

The earliest examination was of one odd specimen on 21st July, 1928, before the weekly examinations had begun. The gonad was so small and unripe that even the sex of the animal could not be determined. At the beginning of August, when the main observations were started, in several cases it was difficult to determine the sex of the animal, since neither males nor females showed any signs of maturity, and the female gonad was small and brown in colour. By the 27th of the month, however, several black ovaries were found, and there were also signs of sperm activity.

Through September the gonads ripened amazingly quickly, and at the end of the month mature specimens of both sexes were found. From then onwards until April 1929, a regular cycle appeared, of spent and maturing gonads in the first week of the month, maturing ones in the middle weeks, and mature ones at the end. The month of greatest activity seemed to be December. By the end of May, however, it seemed quite definitely to be the close of the spawning season, all gonads were small, and the flow was slight. The batch of specimens examined on 18th June showed no large or rayed eggs in females, and no milky flow or active sperms in any of the testes.

EXPERIMENTS.—Apart from the observations just described, experiments were carried out with a view to obtaining supplementary information. Although these experiments could only be done on a small scale, the results were interesting.

Specimens were collected and put into glass jars of 3 litres capacity, one specimen being put into each jar. The mouths of the jars had covers firmly tied over them, made of several layers of butter muslin. This allowed some flow of water into them, but neither

animals nor eggs could escape. The jars were fixed in position by placing them in wooden tubs, which were sunk in the Western Moat, at such a depth that they were always half full of water. The tubs were firmly fastened to the reef and contained wooden partitions, enabling four jars to be fitted into each tub and left there, without any danger of their being broken by waves, etc. In this way jars were left out on the reef sixteen times with perfect safety. The experimental animals were put out on the reef in the afternoon of one day



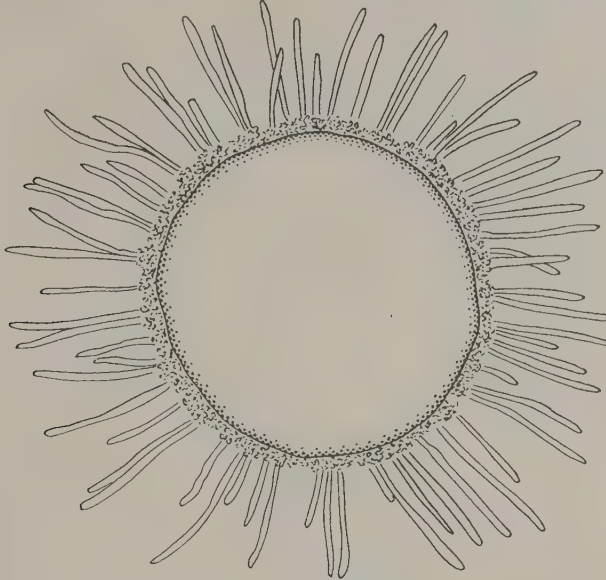
TEXT-FIG. 4.—*Acanthozostera gemmata*. Section of part of a nearly ripe ovary. The young eggs which would mature in a subsequent month are black; the eggs nearly ready for extrusion are stippled. These latter eggs possess rays, which are cut at various angles.

and collected as soon as possible on the morning of the next, when samples of the water in the jars were examined for eggs and sperms.

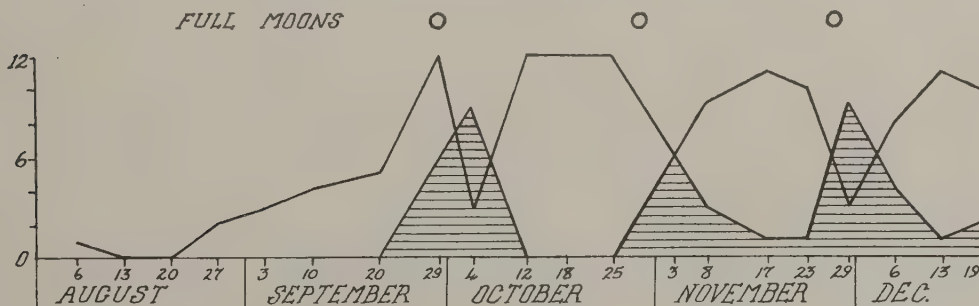
On six other occasions a different method was used as well as the one described above, *i. e.* a number of chitons were collected and kept in buckets of sea-water on the verandah for the night. This method proved less satisfactory than the other.

The dates of these experiments were carefully chosen. In eight cases the experiment was carried out on the night of full moon, and on all these occasions, except the last one (which was in May, after the breeding season), spawning occurred. The specimens which

spawned were always females, except in one instance, when sperms as well as ova were liberated in a bucket containing 6 chitons (27th December). It is possible that none of the males isolated in separate jars shed their sperms, because no female was present with them; the presence of a female in the bucket perhaps provided a stimulus which caused the male to emit spermatozoa. In the case just quoted fertilization had occurred and early



TEXT-FIG. 5.—*Acanthozostera gemmata*. From a camera lucida drawing of a mature egg, extruded on 29th September, 1928. Diameter of egg 120μ .



TEXT-FIG. 6.—*Acanthozostera gemmata*. Graphs showing the number of mature and spent gonads (♂ and ♀) for each week, during part of the year. Shaded graph, spent or partially spent individuals; unshaded graph, mature and maturing ones. A period of maturity occurs in each month at or before the time of full moon and a spent period follows each full moon.

segmentation stages were present. The remaining experiments took place on nights either immediately preceding or following the night of full moon, and on none of these occasions did any spawning occur.

CONCLUSIONS.—The above data show clearly that for several months the animal spawns and recovers every four weeks; after this its activity weakens, the ovaries show no sign of a renewal of their stock of eggs, and gradually the animal enters into its resting

period. During the breeding season the flow of sperms and the fluidity of the female gonad vary markedly with a monthly rhythm; but in the quiescent period the colour and size of the gonads are notably different from their aspect during the months of activity.

It should next be noted that, during the breeding season, the part of each month during which the gonads are mature lies in all cases at or before the time of full moon (see Text-fig. 6); and the experiments show that specimens of the species do actually spawn on the night of full moon. There can therefore be no doubt that the species does spawn at about the time of full moon for several successive months in the year. The fact that in the experiments spawning occurred on the actual night of full moon *only* may, however, have been accidental, and need not be stressed.

TABLE II.—*Spawning Experiments on Acanthozostera gemmata.*

Date.	Condition of moon.	Method.	Number of chiton used.	Result.
1928:				
September 29	Full	Jars	?	Specimens spawned; number not noted.
October 29	"	"	6	2 ♀ spawned.
November 27	"	"	8	2 ♀ spawned.
December 25	"	"	6	0
" 27	Full	"	6	2 ♀ spawned.
" 27	"	Buckets	6	1 ♂ spawned; unknown number of ♀ spawned.
" 28	"	Jars	6	0
1929:				
January 26	"	Buckets	16	0
February 23	"	Jars	7	0
" 23	"	Buckets	5	0
" 24	Full	Jars	7	2 ♀ spawned.
" 24	"	Buckets	5	0
" 25	"	Jars	7	0
March 25	Full	"	6	1 ♀ spawned.
April 23	"	"	8	0
" 23	"	Buckets	6	0
" 24	Full	Jars	7	1 ♀ spawned.
" 24	"	Buckets	5	0
" 25	"	Jars	4	0
May 22	"	"	6	0
" 23	Full	"	6	0
" 24	"	"	6	0
22 experiments.	Full moon on 8 occasions.	Jars 16 times. Buckets 6 times.	139 specimens.	More than 13 positive results.

Cypraea annulus.

Number of specimens used, 490 (208♂, and 282♀).

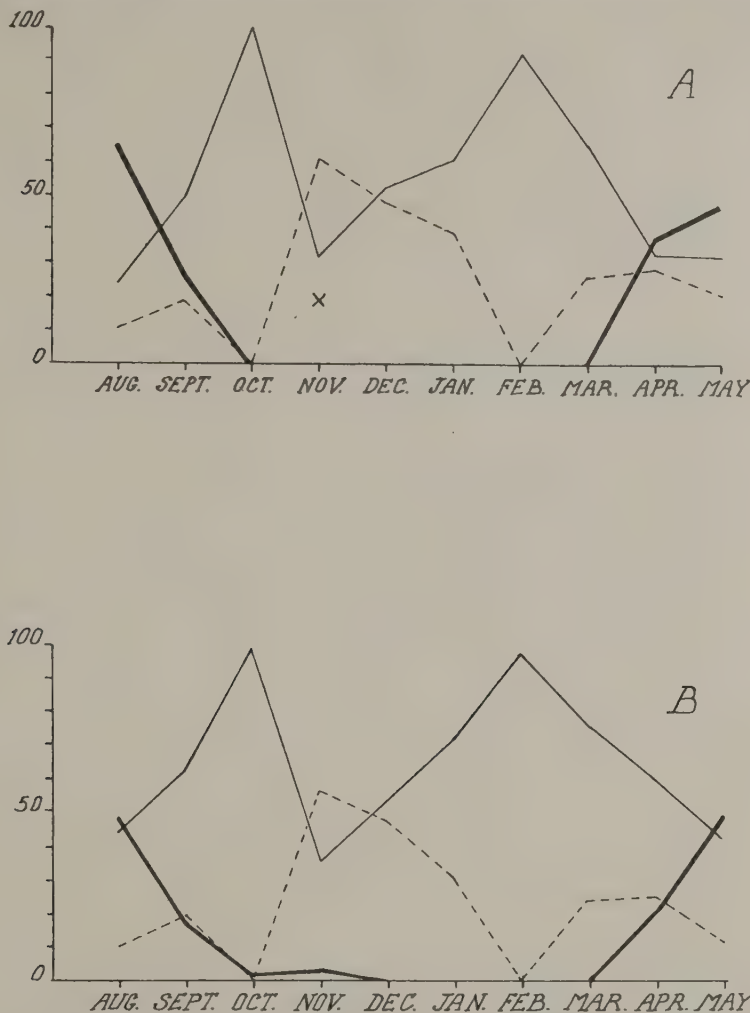
Weekly examination of 12, 9th August, 1928 to 2nd January, 1929; 29th January, 1929 to 30th May, 1929.

One examination on 15th June, 1929.

Average length of animal, 2.35 cm.

Range of size, 1.8–3.6 cm.

The animals were plentiful on many parts of the reef, and those examined were all collected either from *Hippopus* shells in the Mangrove park, or else from amongst the



TEXT-FIG. 7.—*Cypraea annulus*. The graphs in Fig. A apply to the gonads of females only; those in Fig. B to males and females taken together. Thick continuous line, immature; thin continuous line, mature or nearly so; broken line spent or partly spent. The percentage of specimens belonging to each category is shown for each month. Immature specimens are absent or nearly so in the warmer months, at which time spent and mature specimens are most numerous. The drop in mature specimens in November, coinciding with a peak among the spent ones, probably indicates approximately equal numbers of specimens ready to spawn or having just spawned. The cross in Fig. A indicates that in this month the greatest number of spawning individuals was found on the reef. The two series of graphs are given to show the close similarity between the results for one sex only, and for the two sexes taken together; this applies throughout to the cases recorded in this paper.

Thalassia on the flats around the anchorage. The shell, being very hard, was cracked in a vice, when the animal could easily be extracted.

THE MALE GONAD.—The testis was usually easily discernible, shading from a bright

orange to a brown or chocolate colour. The colour seemed to bear no relation to the ripeness or otherwise of the individual, although there might be a tendency for the testis to have a darker appearance towards the end of the spawning season. The sperms, of which there are two types, a normal and a vermiform, never showed the intense activity of those belonging to some other animals examined, nor was there such a plentiful or free flow of them when the testis was cut, even in specimens which were mature. There appeared to be no sudden dispersal of sperms and consequent immediate shrinkage in the size of the testis, as was observed in the case of *Ophiothrix*, for instance, but only a gradual decrease in the quantity and activity of the sperms, and therefore eventually in the size of the gonad. The exact condition of the animal was often difficult to determine in consequence.

THE FEMALE GONAD.—As in the male, the colour of the gonad did not indicate any particular stage in maturity; it was usually cream or yellow, and darkened a little towards the end of the spawning season. Probably several batches of eggs were laid before the animal became exhausted. This final stage was easy to determine, as the ovary then contained only disintegrating and immature eggs, and had become much smaller. At no stage did the eggs wash out very easily.

RESULTS.—After careful consideration of the records, no outstanding breeding and resting periods can be distinguished, and certainly no lunar changes seem to affect the animals. A certain amount of fluctuation in the spawning activity, however, does undoubtedly occur. During August and September the number of immature specimens gradually decreased, and the number of specimens with well-developed gonads simultaneously increased. In October and November mature specimens were numerous, whilst the number of partially spent ones slowly increased. In November there appeared to be a higher percentage of partially spent than of mature ones, but by February ripe specimens once more were dominant. After February the number of mature animals steadily fell, and the number of spent and immature ones rose. By the beginning of May spent specimens were rare, and immature ones commonest. Unfortunately there is only one record in June, when the specimens examined were immature.

CONCLUSIONS.—In spite of the difficulty of interpreting the records, there seems to be little doubt that *Cypraea annulus* had a period of considerable activity during the summer months, possibly lasting from October until the end of February. There seemed to be a less active period during May and June, but possibly no complete resting period. Probably one specimen can spawn more than once in a year. The results of the routine observations on gonads are represented graphically in Text-fig. 7.

Apart from the observations on gonads, *C. annulus* was found spawning on the reef by various members of the expedition; the records of such spawning all occur between October and March, and although there was no systematic hunting, the records verify the supposition that *Cypraea* was spawning in those months. Animals which were spawning or had just spawned were found on 28 occasions.

Hippopus hippopus.

Number of specimens used, 392.

Weekly examinations of 12 or 6, 8th August, 1928 to 2nd January, 1929; 1st February, 1929 to 25th April, 1929.

Further examinations 23rd and 25th July, 1928; 21st and 28th May, 17th June, 1929.

Fifty specimens examined between 1st and 4th February, 1929.

Artificial fertilizations: 47 attempts made on 17 occasions, extending over 7 months, 14th August, 1928 to 14th February, 1929.

Average length of shell, 24.0 cm.

Range of size, 14.4–33.0 cm.

Hippopus hippopus was an excellent mollusc for experimental purposes. It was one of the commonest animals on the reef, and lay about on the flats in hundreds, unattached. The one disadvantage was the weight of the creatures, but two people with a wooden stretcher could collect a dozen specimens comfortably in two journeys.

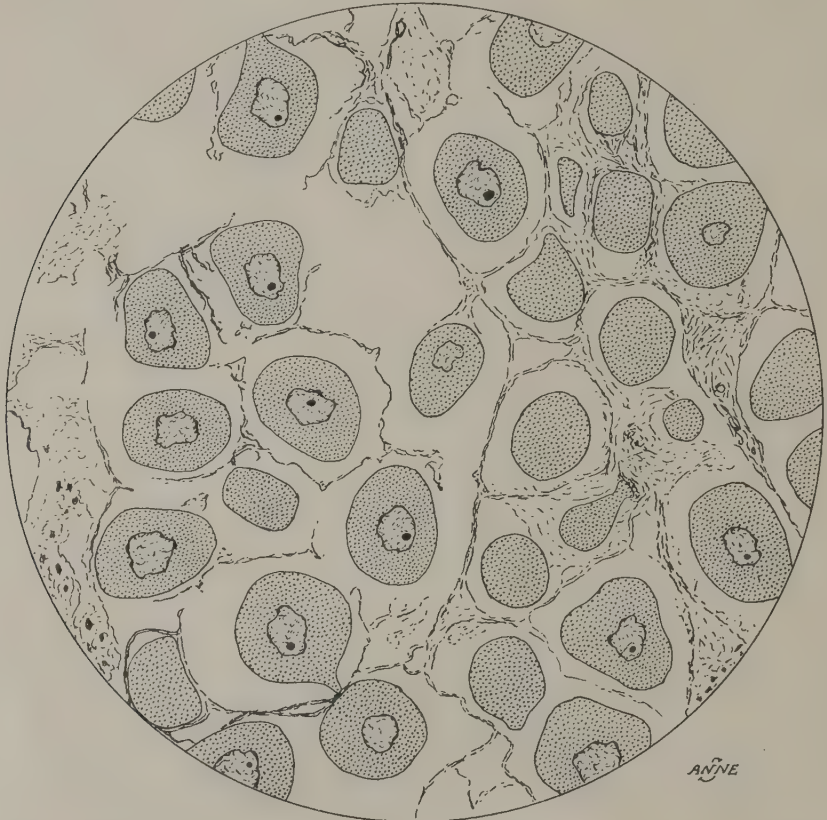
THE GONADS.—*Hippopus hippopus* is hermaphrodite, of the type in which male and female acini lie side by side throughout the whole extent of the gonad (Text-fig. 10). The gonad, when mature (Text-fig. 8), was large and extensive, and light cream in colour. On cutting it there was a copious milky flow, which contained myriads of extremely active sperms, and free eggs with plainly visible nuclei, very often presenting that even appearance as of a field of marbles, so characteristic of samples from mature gonads. The condition of the gonad when spent (Text-fig. 9) was very distinctive; it was much less in bulk, and the cream colour had changed to a dull yellow with opaque patches, giving a mottled granular appearance to the whole organ. It was of a soft liquid consistency, but when cut there was no flow or only a slight clear one, which contained a decreased number of more or less inactive sperms, and irregularly-shaped eggs, often lacking any visible nuclei. On the other hand, an immature gonad was found to be small and of an even cream colour; when cut there was no flow, but the gonad contained numerous immature eggs embedded in tissue, and sperms neither plentiful nor active—the normal condition for an immature gonad.

RESULTS OF ROUTINE WORK.—When the main observations were begun in August 1928, the gonads were in a half-ripe condition, but as the summer approached there were signs of increasing maturity. By November the general aspect of most of the specimens was that of maturity, and on 7th December appeared the first specimen which gave evidence of having spawned. The following week provided two more such examples, but then, unfortunately, owing to absence from Low Isles, the examinations ceased entirely from 2nd January to 1st February, 1929. When the work was resumed on the latter date, it was found that every specimen of the first batch examined seemed to have spawned. To verify this, between the 1st and 4th of February 50 animals were examined, 20 microscopically in the laboratory and 30 on the reef *in situ*. In this latter examination the animals were collected in an entirely haphazard fashion from the Sand and Thalamita flats. These clams were opened, the gonads inspected, and a note made of their condition, which was easy to determine in the case of spent individuals. Of the 30 specimens thus examined, 23 had a positive spent appearance, and 7 were apparently partially spent; of the other 20 examined in the laboratory, 19 seemed completely spent and 1 partially so. Of the whole 50, therefore, 42 were quite spent and 8 less completely exhausted.

For the remainder of February and March, the weekly examinations gave consistent results in which the majority of animals were spent or nearly so. By April, however, no more partially spent specimens appeared, the gonads were small and any flow had

ceased, and they were more solid in consistency. Through May all signs of past spawning disappeared, and the examination in June gave a uniform result of immature gonads.

FERTILIZATION EXPERIMENTS.—Forty-seven attempts were made at artificial fertilizations, on 17 different occasions, between 14th August, 1928, and 14th February, 1929. Eggs and sperms were taken either from different individuals or from the same ones, and placed in bowls of sea-water, usually filtered, for a number of hours, samples being taken from them at intervals and examined microscopically. In no case was a



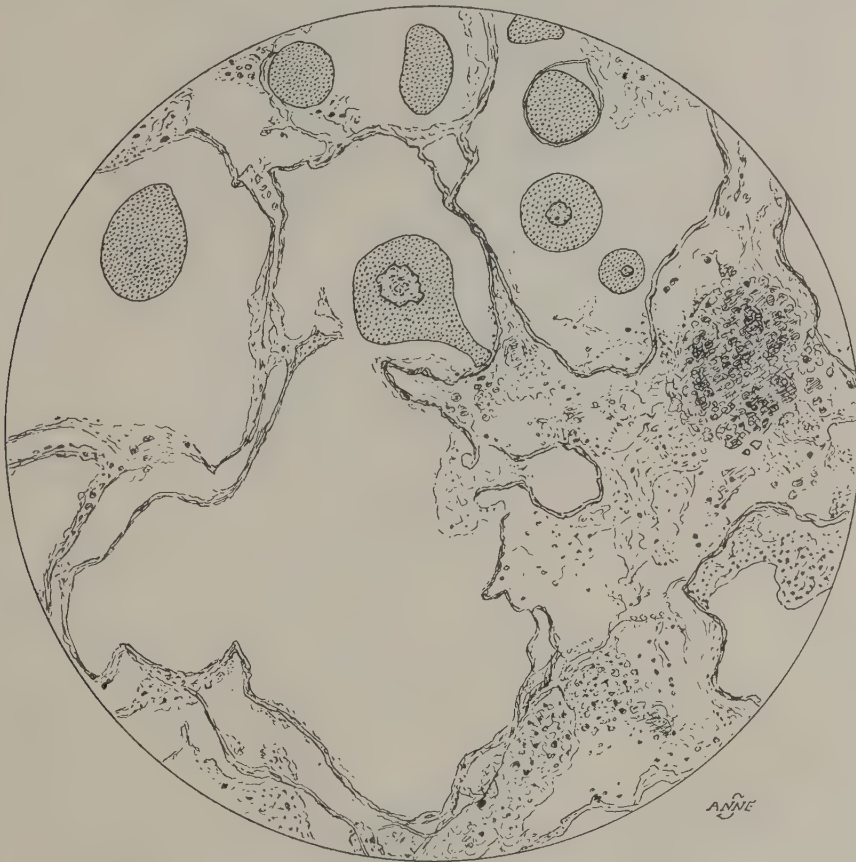
TEXT-FIG. 8.—*Hippopus hippopus*. Part of a section of a mature gonad, for comparison with the section of a spent gonad shown in Text-fig. 9.

completely normal result obtained, which was probably, to a large extent, due to the facts that during the early part of the period the eggs were not sufficiently mature, and later, when the eggs and sperms were in a riper condition, the weather became too hot for success in such work, in a place where there were no adequate means of keeping the finger-bowls cool.

Until the end of November, 1928, the majority of the tests produced early segmentation stages, and frequently quite a high percentage of morulae; on one occasion in November, embryos in some cases had developed cilia. But there were nearly always present obvious abnormalities, and often at quite an early stage all the eggs died. As the spawning period

approached, the fertilizations became unsuccessful because of the heat. The results of these experiments fit in with the conclusions outlined below.

CONCLUSIONS.—From these data we may conclude that probably *H. hippopus* was in an immature condition in the Australian winter (June and July), that it ripened during the months of August, September and October, and that during November, December and January the gonads were mature, or nearly so. Probably some spawning occurred from December to March, since spent specimens could be found in each of these months ;



TEXT-FIG. 9.—For explanation see Text-fig. 8.

but the very high percentage of spent individuals found at the beginning of February suggests that the greater part of the spawning had occurred during January.

From 7th December to the end of the month the surface temperature in the Anchorage, in the afternoon, was always above 28.0 C., rising at its highest to 30.7° C. on the 24th. Probably spawning first began during this period. A second hot spell started on 12th January, and from that date until the 30th the afternoon temperature in the Anchorage was always above 29.0 C., rising at its highest to 31.98° C. on the 19th. In all probability the spawning of the majority of the clams took place during this second still hotter spell. This would be in line with the work of Orton, Nelson, and others who have shown that certain lamellibranch species spawn after the temperature has reached a certain definite level.



TEXT-FIG. 10.—*Hippopus hippopus*. Part of a section of a gonad, showing a group of male acini and a few ova.

Thalamita stimpsoni.

Number of specimens examined, 423 (211♂ and 212♀).

Weekly examinations of 12 specimens (approximately), 10th August, 1928 to 5th January, 1929; 6th February, 1929 to 15th June, 1929.

Average width of carapace, 5.0 cm.

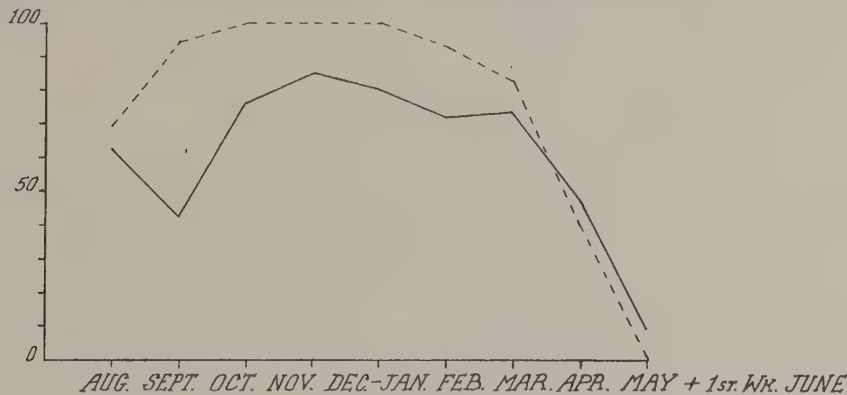
Range of size, 3.2–7.0 cm.

This crab was fairly numerous amongst the rocks and boulders of the reef flat, especially in that part which is named after it, the *Thalamita* flat. As already mentioned, it was not easy to secure a regular supply of specimens, particularly when the tide did not entirely leave the flat, as at neap tides. This is the reason for some of the irregularities in the records of weekly examinations.

The animals were usually collected and examined on the same day; if, however, they had to be kept for a time, for instance when the tide made it only possible to collect them at night, they were stored in covered baskets in the sea. In addition to the examination of gonads, spawn carried by females was examined, and notes taken of the stages of development reached by the embryos.

THE MALE GONAD.—In the case of males it was found that nearly all the specimens contained formed spermatozoa; but from October 1928 onwards an increasingly high percentage of the sperm occurred enclosed in spermatophores, filling the vas deferens. The testes increased in size during the first few months (August to October), but after January 1929, the development slowly became less and less; the vas deferens, however, remained distended with spermatophores.

THE FEMALE GONAD.—At no time during the year was there a period in which females with empty ovaries were numerous; but the condition of the eggs and the size of the gonad showed a definite variation in certain months. In August 1928, when the work began, usually all specimens contained thick and extensive ovaries with maturing eggs. By October there was a higher percentage of individuals with immature ova, and this continued throughout November; the ovaries were still large and extensive. From December to March large ovaries and mature eggs again predominated. After this period,



TEXT-FIG. 11.—*Thalamita stipsoni*. Graphs showing (a) the percentage of females bearing embryos, in each month (continuous line); and (b) the percentage of males with large gonads (broken line). The first graph shows that berried females occurred in every month, but more commonly in the warmer months; the second indicates more widespread activity in the male gonad in the warmer months than in the cooler ones. Occurrence of spermatophores in the male is not included here.

however, an increasing number of specimens showed thin and inextensive gonads (sometimes the ovaries could not be identified at all), containing variously mature or immature eggs. By the end of May nearly all specimens had small gonads containing immature eggs. The one examination in June showed a similar state of affairs.

Females were found carrying embryos from August through to March, the highest percentage of berried crabs being reached in November and December. A marked diminution in the numbers occurred in April, and in May the percentage of berried females is very low, coinciding with the presence of small gonads with immature eggs. Spent females with soft shells occurred intermittently throughout most of the year. The condition of the gonad in the females carrying embryos was somewhat variable; but only in the months when berried females were scarce were the gonads of the majority in a relatively inactive condition.

CONCLUSIONS.—The fact that berried crabs were to be found in every month from August 1928 to June 1929 shows that at least some reproduction occurred during the greater part of the year, if not all of it. At the same time the percentage of females carrying embryos varied markedly, and when plotted for the period of observation shows a fairly regular curve (Text-fig. 11), the percentage in the warmer months being uniformly high. The cycle of changes in the ovaries of the females also indicated greater activity in the warmer months than in the others. The curve illustrating the percentage of males with large gonads (Text-fig. 11) tells the same story. It is true that the males continued to have spermatophores in the vas after the period of greatest activity in the testes was over*; but since spermatophores in Crustacea are sometimes stored for a long time (it is well known that sperms contained in spermatophores may live for months or years carried by the female), their presence does not necessarily imply *recent* testis-activity on the part of the individual possessing them. It seems a fair conclusion that *Thalamita stimpsoni* spawns to a certain extent for most of the year, but that spawning occurs in a much higher proportion of the population in summer than in winter.

SPAWN COLLECTED ON THE REEF.

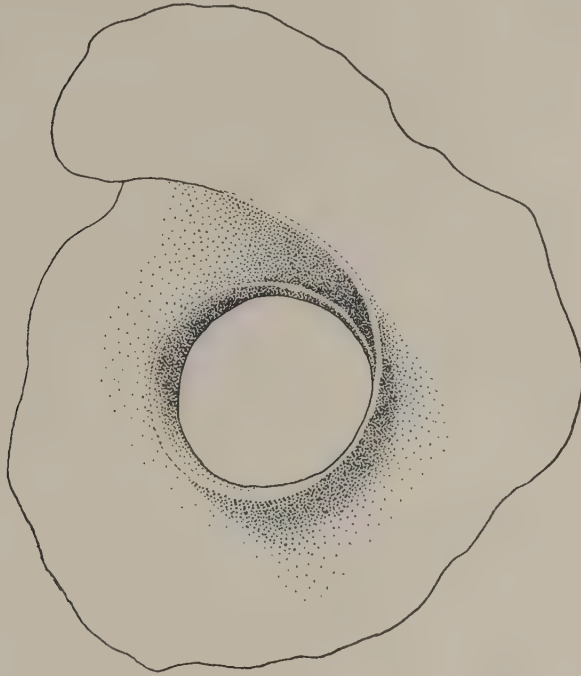
During the year a record was kept of spawn collected on the reef by any member of the expedition. In the case of each specimen the spawn was described and its condition noted. In some cases where the animal was found actually depositing the spawn it was possible to make a definite identification; in other cases only an approximate determination was possible. This collection was not at all systematic, but its results are recorded, since they yield useful data.

The total number of specimens of spawn collected during the ten months, August 1928 to May 1929, was 400, with the addition of many specimens which were recorded simply as "numerous". From the note at the foot of Table IV it will be seen that in each of these ten months at least 8 species of animals were found spawning on the reef. The number for some months was much higher—up to 21 species in October. The fluctuation in numbers from month to month means very little because of the casual nature of the collecting. The number of days in each month on which spawn was collected varied from 5 to 16. It is noteworthy that in every month one or more species of the genera *Natica* and *Uber* (Text-figs. 12, 13) was spawning, and sometimes the spawn-coils of these animals were extremely numerous, much more so than the table would indicate.

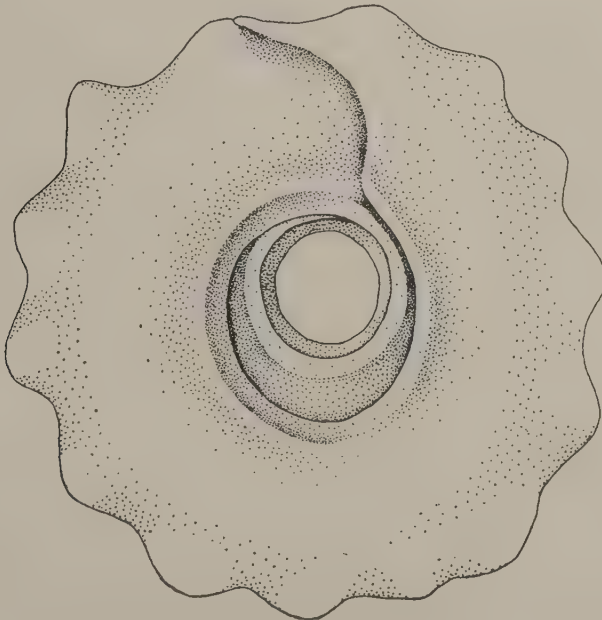
SUMMARY AND CONCLUSIONS.

In this summary, which includes the results described in Parts I and II of this paper, together with those of Moorhouse and Nicholls, a differentiation has been made between facts which are certainly known and those which seem probable, but in the latter case the degree of probability is so high in some cases as to amount almost to certainty.

* From a study of such literature as is available in South Africa, the only record of a probably similar case was found in Andrews, 1911, pp. 428-9.



TEXT-FIG. 12.—This figure and Text-fig. 13 illustrate two sandy coils containing egg-capsules, made by species of *Natica* (or *Uber*); they show the different pattern of coil formed by two distinct species.



TEXT-FIG. 13.—See Text-fig. 12.

During the period August 1928 to June 1929, the following observations were made on the breeding of animals at Low Isles :

COELENTERATA.

Myrionema amboinense.—This hydroid bore gonophores throughout the period ; it produced planulae from March to June, and perhaps in the other months also.

Favia doreyensis.—This coral probably spawned chiefly in December.

Porites haddoni.—This coral spawned continuously from January to July ; there appeared to be a falling off towards the end of this period.

Pocillipora bulbosa.—This coral spawned in nearly every month of the period ; it appeared to exhibit definite lunar periodicity, the spawning periods occurring at about the time of new moon from December to April, and about the time of full moon in July and August, with a transition period in May and June.

Pavona cactus.—A single record of spawning of a male colony of this coral was obtained in November.

ECHINODERMATA.

Ophiothrix longipeda.—This brittle star spawned in February ; its breeding period probably extended from December to February.

Tripleneustes gratilla.—This urchin spawned in April, May and June. Almost certainly it had an earlier spawning period about September to November the year before, with a resting time during December and January.

Centrechinus setosus.—Spawning was observed in December ; the breeding period probably extended from about November to March ; lunar periodicity was suspected, but not demonstrated.

MOLLUSCA.

Acanthozostera gemmata.—This chiton spawned in the months September, October, November, December, February, March and April, at the time of full moon. The gonad samples confirmed the lunar periodicity observed in the actual spawning.

Cypraea annulus.—Spawning in this cowrie occurred in the months October, November, December, January and March. The breeding season probably extended from October to March.

Hippopus hippopus.—Most individuals of this clam probably spawned rather suddenly in January. It is likely that some breeding took place from December until March.

Trochus niloticus.—This gastropod spawned in March, June and July, and probably for a longer time than this (Moorhouse).

Pinctada margaritifera.—(The black-lip pearl-oyster.) According to Nicholls, this species spawned in November and May.

CRUSTACEA.

Thalamita stimpsoni.—This crab spawned throughout the period, but gave clear indications of a particularly active breeding season during the months October to March.

GENERAL.

From the collection of spawn on the reef it was ascertained that during each month of the period at least eight animal species were spawning ; in some months many more than this. The details are given in Tables III and IV, pp. 269, 270.

TABLE III.

A. 1918.	1918.				1919.				1920.				Number of specimens.	Date.	Number of specimens.
	September.	October.	November.	December.	January.	February.	March.	April.							
GASTROPODA.															
<i>Cypraea canaliculata</i>		25	1	8, 10, 23	19	31	3	27	2			4, 27	3		
" <i>arabica</i>		23, 28	2					26	1						
" <i>lyner</i>		27	1									21	1		
" <i>viridula</i>		23	1	22	1			4	1			6, 7	3		
" <i>sp.</i>	24, 25	24	1	26	1										
<i>Conus</i> sp.		23	1	23	1			4, 5	2			23	1		
<i>Lopas vertum</i>		27, 28, 29	7												
<i>Melo diazona</i>	28	1	2												
<i>Natica</i> and <i>Uber</i>	7	17	8	8, 10, 14, 19, 23	21	6, 17, 18, 26, 28, 31	13	4, 29, 30, 31	6			6, 7, 8, 11, 12, 13, 14, 20, 21, 22, 27	31		
(7 species)	30											6, 8, 10, 11, 18, 22, 23, 26, 28, 31	36	3, 4, 6, 12, 16, 19, 20	59
<i>Turbo concinnus</i>															18, 28
<i>Aplysia</i> (?)	24	1	8, 10	22	1	6, 20, 23	3	4, 30	3			8, 31	3	4	
(2 species)				8, 11, 19, 22, 23, 27	7										
<i>Hydatina</i> sp.	27	1				31	1								
Nudibranch	23	1				26	1								
Opisthobranch								24, 28	4			7, 13	8	8	1
(2 species)															26
Opisthobranch (?)	27, 29	2													
Gastropod	30	1	6, 13	3, 10, 22, 23	10	14	1					1, 10, 18, 22, 28	7	6, 12, 14	38
(9 species)					N.										27, 28
Gastropod (?)															
(4 species)			13					27	1			18, 31	2	8, 26	18
CRUSTACEA.															
<i>Cryptochirus</i>		15	2									6	1		
Hermit crab	26, 28											31	3		
POLYCHAETA.															
Polychaets	4, 8	N.	3	N.								28	N.		

* The numbers listed under the months refer to the dates in each month on which the species in question was found. The number of specimens refers to specimens of spawl. N., numerous; S., several.

TABLE IV.

Animal.	Dates.	Number of specimens.
GASTROPODA :		
<i>Cypraea moneta</i>	November 10	1
„ „ (golden)	April 26	1
„ <i>staphylea</i>	October 23	1
<i>Conus textile</i>	November 23	1
<i>Magilus</i>	February 2	1
<i>Aplysia</i>	October 29	3
Aplysiomorph	November 10	1
<i>Dolabella</i> (?)	August 30	1
<i>Hydatina amplustre</i>	November 6	2
<i>Philine</i>	August 29	1
Pleurobranch	October 25	1
CEPHALOPODA :		
Cephalopod	March 31	1
CRUSTACEA :		
<i>Caphyra levis</i>	August 27	2
Crab (?)	August 28	1
<i>Gonodactylus glabrous</i>	November 5	1
<i>Panulirus</i>	December 18	1
<i>Trapezia cymodoce</i>	January 8	1

The number of species spawning in each month was as follows : August, 14 ; September, 8 ; October, 21 ; November, 18 ; December, 9 ; January, 11 ; February, 15 ; March, 14 ; April, 11 ; May, 8.

The following general conclusions may be drawn from the above data.

(1) Breeding of animals was by no means confined to any one part of the year ; it occurred in every month, and therefore in winter as well as in summer.

(2) Examples were found of the following types of breeding :

(a) A single breeding period in the year not lasting the whole year round (*Favia*, *Ophiothrix*, *Hippopus*, *Cypraea*, *Trochus*, etc.).

(b) Continuous breeding throughout the year, but more active in one part of the year than during the remainder (*Thalamita*, and possibly *Myrionema* and *Porites*).

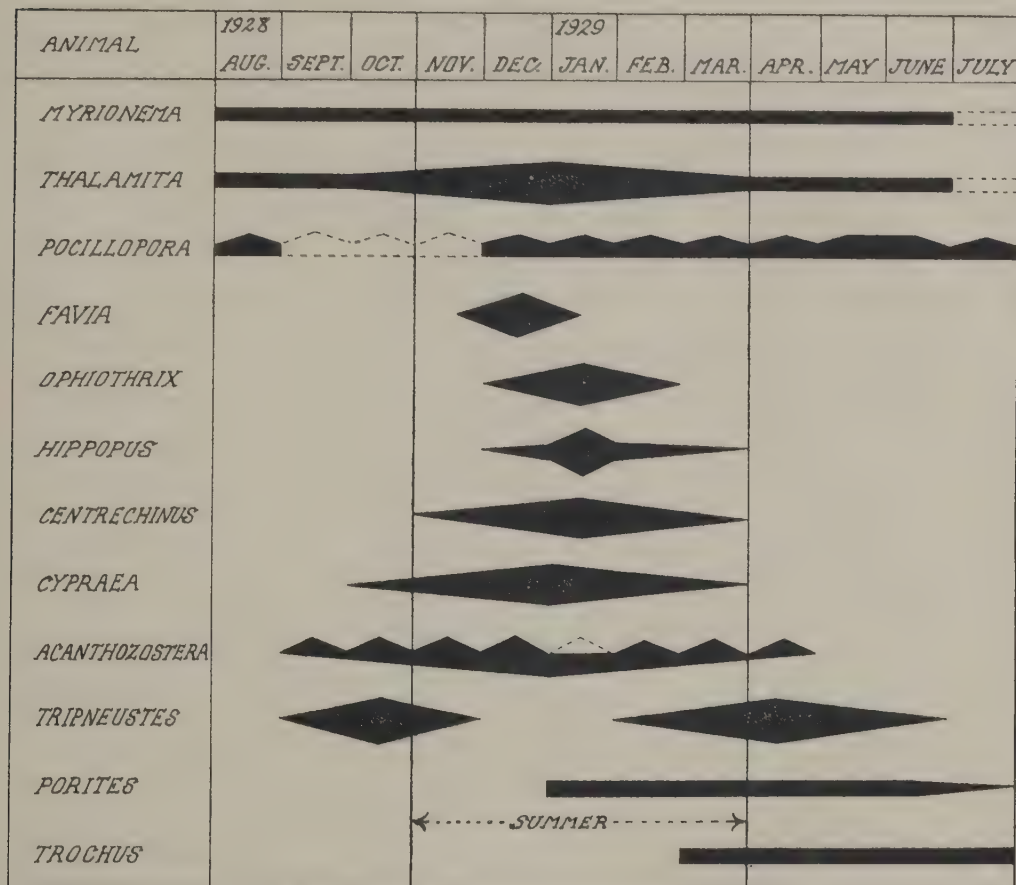
(c) Discontinuous breeding, occurring in relation to lunar phases, during a longer or shorter portion of the year (*Pocillopora*, *Acanthozostera* and possibly *Centrechinus*).

(d) Two spawning periods in the year, with a quiescent phase between them (*Tripneustes* and probably *Pinctada*).

(3) Although some species were breeding at all times of the year, in 7 out of the 13 species specially studied, the breeding period was either contained in or had its maximum in some part of the summer. This is well brought out by the diagram reproduced as Text-fig. 14, in which the breeding seasons of these species are graphically represented.

(4) Summarizing the whole work, it may be stated that on the Low Isles Reef during the period investigated, spawning of animals was going on the whole year round, but that if a census of all species could be made, a majority of them would be found spawning either exclusively or most actively in the warmer months. Probably Low Isles is very typical of tropical marine areas in this respect.

An investigation of wider scope than the present would no doubt add corrections of detail to the conclusions here set out. Especially, the actual breeding-season of any one species would probably fluctuate considerably from one year to another, in the same place, not to mention its varying from one district to another; but the broad conclusions here stated are well founded, and can be amplified as new information comes to hand.



TEXT-FIG. 14.—Diagram indicating the probable spawning periods of the species specially studied at Low Isles, as described in the summary. Broken lines show probabilities where there are no data. Periodicity is indicated by a succession of peaks (the peaks not adjusted to moon phases). In the cases of *Thalamita* and *Hippopus* the wider part of the figure implies increased breeding activity; in the plain diamond-shaped figures the shape is purely conventional, and indicates simply the *duration* of the breeding period; i.e. the widest part does not imply the most active part of the period. In the case of *Porites* and *Trochus* the figure starts abruptly, since the beginning of the period is unknown.

This paper might be made an opportunity for discussing the general question of lunar periodicity; especially since two new records are made of the occurrence of this phenomenon, and one of them appears to be of a novel character (*Pocillopora*). Since, however, we have at present no new theory to suggest which will account for all the facts,

and as these facts have been summarized elsewhere, no further comment will be made. Recent literature on periodicity is listed in Part I.

When the plankton-work of the expedition is published, further information will become available. No reference is made to plankton in this paper since very few of the results have as yet been printed.

REFERENCES.

For further references see Part I of this paper, p. 243.

- ANDREWS, E. A. 1911. Sperm Transfer in Certain Decapods. *Proc. U.S. Nat. Mus.*, Washington, 39, pp. 419-434, text-illustr.
- FASTEN, N. 1917. Male Reproductive Organs of Decapoda, with Special Reference to Puget Sound Forms. *Pub. Puget Sound Mar. Stat.*, Seattle, I, pp. 285-307, 5 pls.
- FOX, H. M. 1924. Lunar Periodicity in Reproduction. *Proc. Royal Soc.*, London, B, XCV, pp. 523-550, text-illustr.
- FRASER, E. A. 1931. Observations on the Life History and Development of the Hydroid *Myrionema amboinense*. *Sci. Rep. Gt. Barrier Reef Exped. 1928-29*, London, III, pp. 135-144, 3 pls., text-illustr.
- LO BIANCO, S. 1909. Notizie biologiche riguardanti specialmente il periodo di maturita sessuale degli animali del golfo di Napoli. *Mitt. zool. Stat. Neapel*, XIX, pp. 513-763.
- MAYOR, A. G. 1914. The Effects of Temperature upon Tropical Marine Animals. *Pap. Dept. Mar. Biol. Carn. Instn. Wash.* VI, pp. 1-24, text-illustr.
- MOORHOUSE, F. W. 1932. Notes on *Trochus niloticus*. *Sci. Rep. Gt. Barrier Reef Exped. 1928-29*, London, III, pp. 145-155.
- NELSON, T. C. 1928. Relation of Spawning of the Oyster to Temperature. *Ecology*, Brooklyn, IX, pp. 145-154, text-illustr.
- NICHOLLS, A. G. 1931. On the Breeding and Growth-rate of the Black-lip Pearl Oyster (*Pinctada margaritifera*). *Reports of the Great Barrier Reef Committee*, Brisbane, III, No. 2, pp. 26-31, 2 pls.
- ORTON, J. H. 1920. Sea-Temperature, Breeding and Distribution in Marine Animals. *J. Mar. Biol. Ass. U.K.*, Plymouth, XII, pp. 339-366, text-illustr.
- 1926. On Lunar Periodicity in Spawning of Normally Grown Falmouth Oysters (*O. edulis*) in 1925, with a Comparison of the Spawning Capacity of Normally Grown and Dumpy Oysters. *J. Mar. Biol. Ass. U.K.*, Plymouth, XIV, pp. 199-225, text-illustr.
- PLYMOUTH MARINE INVERTEBRATE FAUNA. 1931. *J. Mar. Biol. Ass. U.K.*, Plymouth, pp. 1-371.

ECOLOGICAL SURVEYS OF CORAL REEFS

BY

S. M. MANTON, Sc.D.,

Demonstrator in Comparative Anatomy in the University of Cambridge and Fellow of Girton College

WITH AN INTRODUCTION BY

T. A. STEPHENSON, D.Sc.,

Professor of Zoology, University of Cape Town

WITH TWO TEXT-FIGURES AND SIXTEEN PLATES.

CONTENTS.

I. A QUANTITATIVE ECOLOGICAL SURVEY OF TRAVERSES ACROSS LOW ISLES REEF.

	PAGE
INTRODUCTION (by T. A. STEPHENSON)	274
PREVIOUS WORK	276
POSITIONS OF SURVEYS ON LOW ISLES AND METHODS EMPLOYED	276
THE SURVEY OF TRAVERSE I	279
Physical Conditions along Traverse I	279
Detailed Account of the Substratum, Corals and Algae of Traverse I	281
(1) The Thalamita Flat	282
(2) The Moat	282
(3) The Boulder Tract	285
(4) The Seaward Slope	286
(5) The Sea Floor	290
THE SURVEY OF TRAVERSE II	290
Physical Conditions along Traverse II	291
Detailed Account of the Substratum, Corals and Algae of Traverse II	291
(1) The Beach Sand	291
(2) The Beach Sand-rock	291
(3) The Inshore Part of the Reef	292
(4) The Seaward Slope	293
THE SURVEY OF TRAVERSE III	297
DISCUSSION AND CONCLUSIONS	298

II. DESCRIPTION OF SMALL AREAS ILLUSTRATING THE CORAL FAUNA ON CHARACTERISTIC ZONES OF AN OUTER BARRIER REEF (YONGE REEF).

	PAGE
REEF CREST	304
OUTER MOAT	305
INNER PARTS OF THE REEF	306
SUMMARY	307
REFERENCES	308
TABLES OF LEVELS ALONG THE TRAVERSES	309

I. A QUANTITATIVE ECOLOGICAL STUDY OF TRAVERSES ACROSS LOW ISLES REEF

INTRODUCTION.

By T. A. STEPHENSON,

Professor of Zoology in the University of Cape Town.

WHEN planning the ecological work which was to be carried out at Low Isles, I had in mind two lines of investigation connected with the estimation of the populations of the reef. The first was to make a general survey of the whole area in order to determine the broad outlines of the distribution of organisms, and their relation to the several available habitats and to the conditions prevailing therein. The result of this survey has already been published in this volume (Vol. III, No. 2). The second objective was to make quantitative surveys of a number of selected strips or patches of the reef, so that the general survey might be illustrated by accurate examples showing exactly and in detail how the organisms were arranged in some of the typical habitats. Originally we hoped to survey patches of sand and mud (sifting out and counting their inhabitants), as well as regions where the substratum is mainly rocky; but shortage of time put an end to this possibility, and permitted us only to survey the surface-life along two narrow strips of the reef.

The two traverses studied both lie on the leeward side of the reef. It would have been very instructive to compare a section down the windward slope with another across the leeward slope; but in practice this was impossible, because the weather conditions at the windward side are normally too windy to permit one to work there, and it could only be done by choosing days here and there over a longer period than was available to us.

The two sections worked were chosen for the following reasons: Traverse I illustrates very well the contrast between the growth of corals and algae which can exist under the somewhat stringent conditions prevailing in a moat (see Vol. III, No. 2, p. 45), and that which is to be found on a slope open to the sea at all states of the tide; it also includes areas of the reef-flat and boulder-tract. Traverse II (leaving out of account the small areas of beach-sandstone and moat which it first crosses) is approximately comparable to the seaward-slope portion of Traverse I, but with modifications, since it is divided rather sharply into a slightly higher landward part and a lower seaward portion, terminating ultimately at a depth of $5\frac{1}{2}$ feet below datum. The landward part crosses and corresponds

to the region of Luana Reef marked A1 on the key chart of Low Isles published in Vol. III, No. 2, Text-fig. 2; the seaward part crosses and corresponds to the area A2. The landward portion uncovers at any tide which falls to a level 0.8 feet above datum; the seaward part is submerged at such a tide, but at the lowest springs (the extreme recorded being 0.4 feet below datum) its highest parts are exposed; its deeper regions are therefore always submerged. The region A1, therefore, as a result of its level, is exposed or awash more frequently and for longer periods than the area A2, though submerged at neap tides. The fall in level from A1 to the beginning of A2, although so slight, is reflected in the coral fauna, the response to the improved conditions being immediately apparent, and being maintained, of course, to the end of the traverse, as the level continues to fall. This improvement of the fauna at a critical level is one of the most interesting points illustrated by the traverse. (See also Vol. III, No. 2, p. 62, and Pl. XIV.)

Both traverses have the advantage of crossing regions in which observations on the periodic physical and chemical changes in the environment were made by A. P. Orr. In order to make the data available as complete as possible, level-sections along both traverses were taken by M. A. Spender. Nothing is more evident in modern ecological work than the necessity for correlating details connected with the arrangement of organisms with accurate determinations of level, more especially in the intertidal zone, where slight changes of level involve important modifications in the range of exposure to which organisms are subjected.

It will be noticed that most of the data which follow refer to corals and algae only. A more comprehensive survey in the time available was impossible. The omission is in fact less considerable than might at first appear, since the corals and algae are undoubtedly the dominant organisms in the areas studied. The work must therefore be regarded as a survey of the *principal sedentary oxygen-producing organisms in areas of mainly rocky substratum*. (The production of surplus oxygen takes place, of course, only during daylight.)

The work was started by several of us in the survey of a patch on Batt Reef, in 1928. This taught us the proper method both of making the counts and of representing the result graphically in the way adopted for the plates illustrating this paper. Later on I chose two suitable traverses at Low Isles, and when Dr. Fraser and Dr. Manton joined the expedition, I asked them if they would take over the detailed survey of these. This paper is the outcome of their work. The counting of organisms was carried out jointly by Dr. Fraser and Dr. Manton; but Dr. Manton is solely responsible for drawing up the following report. We are indebted to Miss K. Cole for assistance in the redrawing of the coral maps for the plates.

The algae collected in connection with this work have been determined by G. Tandy. For the names of the corals Prof. Matthai* and I share the responsibility. I have worked carefully through a series of dried specimens in order to check the conclusions as to the identity of the species which were made in the field, and to correlate our determinations with those of Prof. Matthai. A set of specimens held by us to be typical of the species here mentioned will be deposited in the British Museum (Natural History).

* [It is to be regretted that Prof. Matthai, after supplying the names used in this report, found himself unable to complete the systematic examination of the corals. It is hoped to publish later a systematic report on the group by another hand, but any divergences from the nomenclature adopted here will be specially noted.—W. T. CALMAN.]

PREVIOUS WORK.

The more important existing records of detailed examinations carried out on restricted areas of coral reefs are those by Mayor (1918 and 1924) on the fringing reefs of Maer Island, near the northern end of the Great Barrier Reef, and Tutuila, in Samoa, that by Baker (1925) on a fringing reef in the New Hebrides, and the short account by Hedley and Taylor (1907) of a traverse across East Hope Isle within the Great Barrier Reef. The three fringing reefs have land of some height behind them, and present an entirely different structure from that of Low Isles Reef, besides differing somewhat from one another. Thus features of interest brought out by the examination of these reefs cannot be compared directly with conditions on Low Isles. East Hope Isle, like Low Isles, is an "island reef", but the traverse across the former records only the outstanding forms growing on the various parts, and levels were not determined.

Of the traverses across fringing reefs, that across a New Hebrides fringing reef, half a mile in width, records the approximate abundance and zoning of the dominant corals across the reef-flat, coral growth being most abundant near the shore where *Montipora ramosa* and *Goniopora* are dominant. A barren "boulder zone" lies near the seaward edge, and the survey was not continued down the outer slope. The Maer Island fringing reef on the weather side of the island bears a "lithothamnion ridge" on its seaward edge 1800 feet from the shore; while the Aua reef, Tutuila, is bounded seawards at 855 feet from the shore by a rich acropore zone. The reef flats of both are somewhat similar. The numbers of corals occurring on a 50-foot-wide strip at Maer Island and on a 24-foot-wide strip at Tutuila were recorded. Both show a maximum coral growth some distance behind the edge of the reef in relatively quiet water, where the surge dies out, but the maximum variety of corals is found close behind the edge. A zoning of corals is present, but 90% of the colonies consist of four genera—*Porites*, *Acropora*, *Pocillopora* and *Seriatopora*—with *Psammocora* replacing *Seriatopora* on the Aua reef, Tutuila. The main factors concerning the distribution of corals were considered to be temperature, silt, the mechanical effects of moving water and a struggle between species. The algae were few and were not considered quantitatively.

POSITIONS OF SURVEYS ON LOW ISLES AND METHODS EMPLOYED.

On Low Isles a survey was made along Traverse I, shown on the map in Text-fig. 1, lying across the leeward side of the reef. The traverse extends from the outer edge of the Thalamita Flat across the edge of the reef and down its seaward slope until coral growth ceases and the muddy sea bottom is reached. The richest coral-bearing areas of the reef, those of the Moat and of the Seaward Slope, are thus encountered, besides the more barren reef flat and Boulder Tract. It was possible to complete the survey down the seaward edge of the reef to the lower limit of coral growth owing to the small depth at which the muddy sea floor is encountered on the leeward side.

A second survey was made along Traverse II (see Text-fig. 1) from the beach of the sand cay across the end of the Northern Moat, and passing over the reef to terminate on a barren sandy stretch.



Published by permission of the Royal Geographical Society

TEXT-FIG. 1.—Low Isles, from Spender's survey, showing the positions of the Traverses which were surveyed in detail. Traverse I passes from the Thalamita Flat across the Moat and Boulder Tract, and Traverse II passes from the Beach of the sand cay across the reef towards the Anchorage. Part of the area enclosed by a ring in the Madrepora Moat is shown in the large-scale map on Plate X, and part of the Western Moat crossed by the Traverse is shown in Plate I. Traverse III passes through E beacon in line with the lighthouse and traverses the seaward edge of the reef.

A strip of reef one yard in width was examined along each of the traverses. Measurements of levels and distances were carried out by M. A. Spender. Positions and distances along the traverses are given in feet from the beginning of each traverse, and levels are given in feet above or below datum level.* Each traverse was marked out by a series of stakes driven into the reef, a cord being stretched between them. Measurements along the ground were taken with a steel tape, the probable error of the methods employed not exceeding 1/10 foot per 100 feet. Levels were determined with a Watts-Zeiss reversible level, the readings being taken to the nearest 1/100 foot. The probable error does not exceed 0.03 foot per mile. A rectangular wooden frame 1 × 2 yards and cross-partitioned into square feet was placed successively along the traverse, and all the corals and algae occurring on every square yard of reef were recorded. Counts of species occurring on each square yard were made as far as possible, but extensive colonies were recorded in terms of the size of the area covered. Only the presence or absence of many of the smaller algae was noted, and an approximate estimation of their relative abundance per square yard was made. All exposed surfaces were examined, and as far as possible the crevices and hollows in the rocks, but large slabs of rock were not lifted.

On the Seaward Slopes of the reef measurements were made with the steel tape, so far as possible along the contour of the ground. The methods we used permitted an error of about 2 feet per 100 feet, and deeper than 10 feet the readings are likely to be in error by ± 1 foot. In water deeper than about 4 feet measurements were made by sounding. The survey from about 3 feet below datum onwards was carried out by means of a diving helmet. The line of the traverse below the water was maintained by dropping a rope, with an anchor at each end, so that it lay in line with the stakes marking the traverse across the reef flat. As the bottom was very uneven, short lengths were used between the anchors, and the line was carried successively seawards. The wooden frame was suitably weighted so that it would sink easily, and the record of the survey of each square yard was made in pencil on sheets of white ground-glass. Ground-glass was found to be far more serviceable than slates for use under water, as the pencil marks do not rub off easily. The width of the traverse is admittedly narrow, but owing to the difficulties of manipulating a large frame single-handed under water, and to the limited time available, no greater width could be attempted.

A third survey was made along Traverse III (Text-fig. 1) across the S.E. windward edge of the reef. Owing to lack of available time and suitable weather conditions this survey was not quantitative, and was much less detailed than the other two. However, it serves to contrast the seaward slopes on the leeward and windward sides of the reef, and may be compared with the windward edge of the Outer Barrier Reefs.

Finally large-scale maps of small portions of the traverses were made with the help of the wooden grid frame used for counting the organisms on the traverses. Small areas up to 20 square yards were also mapped in the Madrepore Moat, in the Anchorage and on the vertical face of a coral patch, so that ready comparisons of these different coral-bearing regions could be made.

* Datum level is that of low water springs as determined by H.M.S. "Penguin" in 1905, and lies at 17 feet 2 inches below the top of the lighthouse steps.

THE SURVEY OF TRAVERSE I.

The position of this traverse is seen in Text-fig. 1, and a level section along it together with sea-levels are given with the graphs showing the distribution of organisms (Plate I). In Text-fig. 2, *a*, a section is shown passing seawards beyond the end of the traverse. The vertical and horizontal scales are here equal. The reef here is covered at high-water springs by about 7 feet of water. From the edge of the Thalamita Flat the traverse passes through the deeper parts of the Western Moat, over the Boulder Tract, and down the outer slope to the muddy sea bottom at a depth of about 20 feet below datum. Thereafter an even, gentle slope descends to 37 feet below datum at about 1600 feet from the beginning of the traverse (see Text-fig. 2, *a*). The Boulder Tract forms the highest part of the traverse, and at low spring tides is dry between 703 and 826 feet. On its seaward side the water level alters directly with the state of the tide. Within the Boulder Tract, on the other hand, water becomes held up, so leaving the Moat flooded and shallow pools of water standing on the flat, while the water ebbs to a lower level outside. Water remains held up in the Moat for a maximum period of $5\frac{1}{2}$ hours, and lies at a minimum of 2.7 feet above datum (see level section).

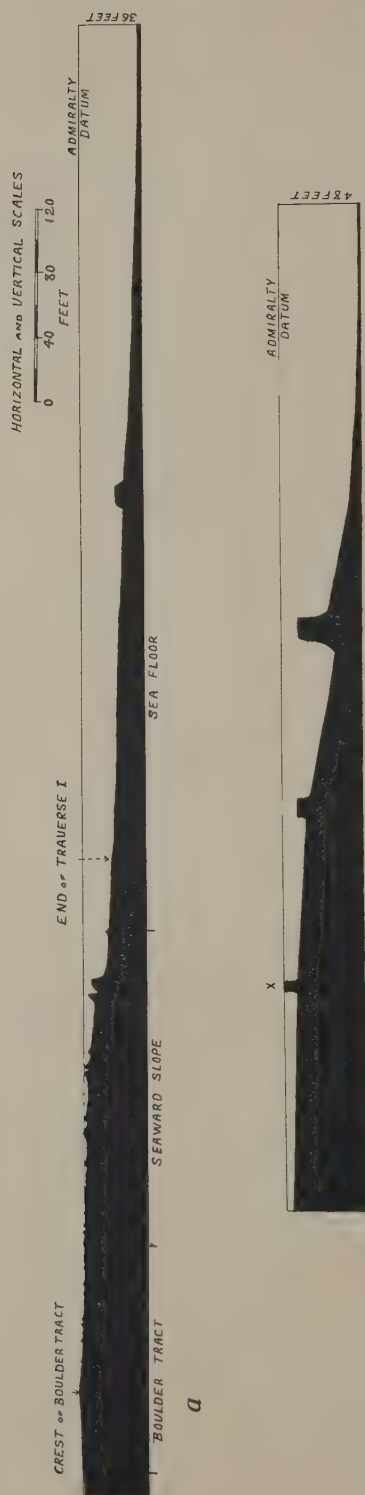
The traverse may conveniently be divided into the following portions for subsequent consideration: (1) The *Reef Flat*, 0–25 feet, is left dry at low water, and lies at about 2.8 feet above datum. The traverse then merges into (2) *The Moat*. The shallower part of the moat extends to 250 feet, and has an uneven bottom at about 2.4 feet above datum. The deeper part of the moat follows, with the bottom at a minimum of 1.8 feet above datum and extends to 700 feet; its floor is uneven, and the deepest parts lie near the Boulder Tract between 515 and 640 feet. (3) The *Boulder Tract* emerges by a gentle slope from the Moat, not by a precipitous scarp as found at the junction of the rampart (Spender, 1930, p. 197) and the other moats. From its crest it slopes downward to 846 feet at about 1 in 25, but the surface is interrupted by projecting boulders. Beyond lies (4) the *Seaward Slope*, a permanently submerged region of large boulders, coral heads and luxuriantly growing coral extending to 1045 feet. The reef profile from the crest of the boulder tract is convex up to 1014 feet, and the downward slope gradually steepens to about 1 in 14. A steeper slope next descends to 1045 feet, dropping steeply at first and then at a slope of about 1 in 9. (5) The mud-covered *Sea Floor* is reached at about 1045 feet. Only the beginning of this region was surveyed where the slope is about 1 in 27.

PHYSICAL CONDITIONS ALONG TRAVERSE I.

Some of the main physical conditions prevailing along the traverse which may influence reef organisms may now be considered. These are correlated with the levels of the traverse which have already been noted, and the manner in which water is held up in the moat at low tide. Tidal and diurnal changes are of much greater importance than seasonal variations.

The conditions within and without the Boulder Tract at low water are very different, and on the reef flat show very large diurnal and seasonal differences. Within the Moat the water is almost stagnant, whereas outside calm and rough water alternate according to the weather.

The Boulder Tract is swept by the broken-water surface, and the higher rocks and



TEXT-FIG. 2.—Level sections across the edge of Low Isles reef, vertical and horizontal scales being equal. (a) Section along Traverse I from the edge of the Moat across the Boulder Tract and Seaward Slope, passing over the Sea Floor beyond the end of the Traverse. (b) Section along a line extending through C beacon and B beacon (see Text-fig. 1) and projected across the reef edge and over the sea floor. The section starts at 390 feet seawards of B beacon. "X" marks the Coral Head, which is shown in the large-scale map on Plate XII. It is clear that the downward slope is more gradual on the leeward side of the island (a) than on the northern side (b).

coral heads outside it are always freely exposed to moving water. Below a depth of 7 feet below datum water movement usually appears to be lessened, and a considerable amount of sediment in the form of fine grey mud lies on rock surfaces in increasing thickness down the reef slope. Details of the composition and deposition of sediments on Low Isles are given by Marshall and Orr, Vol. I, No. 5 of these reports. In the Moat considerable sedimentation takes place, but sediment collected in jars appears to arise mainly from a to-and-fro movement disturbing the moat sand, rather than from actual new deposition. This shifting sediment has here buried and killed the bases of many of the larger corals. Seaward of the Boulder Tract the rate of sedimentation is usually less than in the Moat. In both localities the sediment is composed of sand and fine detritus or mud. In the Moat the bulk of the sediment (95%) is composed of coarse calcareous material. Outside the Boulder Tract much more fine material is deposited, the mud containing a high but variable percentage of non-calcareous matter.

The ranges of temperature in the moat and outside the Boulder Tract are very different. The outside water at a depth of 1 metre fluctuates between about 20° C. in winter and 31° C. in summer, with a daytime rise of 0.3–2.5° C. Within the Moat the daily temperature range is much greater, approximating more closely to air temperatures. In the daytime in the summer the Moat may reach 37.5° C. and at night in winter 18° C. During low water there is no circulation of water into the Moat from outside which might modify the temperature extremes, but since there are two sets of tides a day the temperature seldom reaches levels at which corals cannot survive.

The composition of water inside and outside the Boulder Tract (see Orr, Vol. II, Nos. 3 and 4) at low water is different. Diurnal changes in the Moat are greatest at spring tides and least at neaps. The outside water is more uniform, and at a little distance from the reef shows little diurnal variation. In the Moat during the daytime low water there is a variation in salinity, oxygen content, pH and excess base. During the winter salinity changes are unimportant, and evaporation may cause a rise from 35‰ to 36‰. During the summer, after heavy rain the maximum reduction was to 17‰ in a sandy pool containing little coral on the Reef Flat. The lowest record for the deeper part of the Moat was 27‰, but that was not on an extreme occasion. The lowest oxygen content recorded was 18% saturation and the highest 278%. The pH falls at night and rises during the day, the range being 7.8–8.9. (Full details of variations in the Western Moat and elsewhere are given by Orr in Vol. II, No. 4 of these reports.)

The amount of food available for corals in the form of plankton (see Russell and Colman, elsewhere in these reports) shows no striking difference in richness in the water over the reef flat and beyond the edge of the reef. When the tide is high there is plenty of plankton immediately over the coral, both in the day, when the light is bright, and at night when the coral is feeding. Most of the reef-flat plankton appeared to be similar in quality and relative quantity to that found 3 miles from the reef. However, during periods of low water the small volume retained in the moats must greatly reduce the available plankton.

DETAILED ACCOUNT OF THE SUBSTRATUM, CORALS AND ALGAE OF TRAVERSE I.

The distribution of corals is little affected by the seasons, but the algal growth varies considerably during the year. The survey was made during April–July, 1929, so that details of algae refer to these months only.

Graphs 1-40 (Plates I-IV illustrate the total numbers of coral colonies and also the numbers of species of corals and algae on each square yard of the traverse. Where branching corals are recorded in terms of the area covered, one square foot of coral for numerical purposes has been taken as equivalent to one separate colony. Many species of *Favia*, *Leptastrea*, *Goniastrea* and *Coeloria* will collectively be referred to as *Favia*. Algae which could not be counted individually are represented graphically as present or absent on each square yard. Some of the smaller algae whose distribution and identification is uncertain will not be mentioned.

Unless otherwise stated the descriptions below refer to conditions prevailing at low water.

(1) *The Thalamita Flat.* 0-25 feet. 2.8 feet above datum.

The exposed reef flat is uneven with flat slabs of coral rock, small boulders and fragments scattered on the sand, and water lying in the shallow sandy puddles between the rocks. A few living *Hippopus* (Graph 4) are present, projecting well out of the water.

The rocks are covered by minute and encrusting algae, and the flowering plant *Thalassia Hemprichii* is scattered in the sandy puddles (see Graphs 1 and 5). The most conspicuous elements of the flora are the red algae, mainly *Acanthophora spicifera*, which together with *Laurencia papillosa* and *Roschera glomerulata* form a dense covering on the rocks a few inches in length, but the exposed *Hippopus* shells are not overgrown by algae of appreciable size. Brown algae are small and few, being represented mainly by *Turbinaria* and occasional large and small tufts of *Padina* on the rocks (see Graphs 9 and 10). Green algae are more conspicuous than the brown. *Boodlea paradoxa* and *Halimeda Opuntia* occur on nearly every square yard, the former often quite luxuriant, but *Halimeda* only as poor tufts. *Dictyosphaeria favulosa* and other species of the genus are also fairly abundant.

Corals are entirely absent from the first three yards of the flat. Towards the moat in the puddles three small knobs of massive *Porites* are present 1-2 inches in diameter (see Graphs 2, 3 and 19).

(2) *The Moat.* 25-700 feet. 2.4-1.8 feet above datum.

The moat gradually deepens and then shoals fairly suddenly on to the Boulder Tract (see level section). In the shallower part the water is 0.2-0.4 feet deep, and in the deeper part reaches 0.9 feet. The bottom is uneven and sandy, and bears occasional submerged or slightly projecting slabs of coral rock and small fragments. Salinity, temperature and other changes are at a maximum in the shallower part of the moat.

The outstanding features of the moat are the abundance of algal growth in the shallower part (see Graph 1), and in the deeper part the occurrence of flat-topped platforms of living coral formed by both massive and branching forms which cover much of the bottom (see level section, Graph 16, and large scale map, Plate IX). The area covered by such platforms increases as the moat deepens. Dead massive coral platforms provide sites for fresh coral growth upon their sides (see Plate IX). *Hippopus* occur only in the shallower part (see Graph 4), and its shells form sites for the growth of algae and small corals. Near the Boulder Tract the narrow zone of shallow water does not support abundant algae as does the wider zone of shallow water towards the Flat.

The sandy areas are most thickly covered by *Thalassia Hemprichii* in the shallower

part, and as the available spaces become reduced as coral growth increases, so the abundance falls off (see Graph 5: the uneven peaks on the graph are caused by the alternation of sandy and more rocky areas). *Thalassia Hemprichii* is not found in the sand between the richest coral growth. *Halophila ovalis* appears between 125 and 513 feet, and becomes increasingly common in the sand along with *Thalassia Hemprichii*.

The abundance of algae reaches a maximum at 150–183 feet in the middle of the shallower part, and then progressively decreases as the moat deepens, where algae no longer form a conspicuous living component on the reef (Graph 1). Microphytic algae cover the rocks, and the submerged *Hippopus* shells are densely covered by algae.

In the shallower part, as on the flat, the red algae *Laurencia papillosa* (Graph 12), and *Acanthophora spicifera* (Graph 14) form a large proportion of the algal growth, reaching a maximum at 150–180 feet. As the water deepens slightly, others, such as *Amphiroa fragilissima* (Graph 13) and *Laurencia obtusa* (Graph 15), appear in increasing quantity, but in the deeper part all these species decrease in size and abundance as illustrated by the graphs. *Roschera glomerulata* (Graph 11) on the contrary progressively decreases beyond the flat. *Corallopsis* (?) and *Galaxaura*, however, are found discontinuously along most of this section up to 644 feet.

The largest of the brown algae, *Sargassum lanceolatum* and other species, are attached to rocks in the shallower part, and soon reach their maximum size at about 60 feet (Graph 8). Where suitable rock sites are available up to three large plants about 2.6 feet long may be present on one square yard. Further along the traverse they decrease in size, although the small plants present may be more numerous; *Hydroclathrus* occurs occasionally and other brown algae become more frequent. *Padina* (Graph 9) reaches its maximum density between 215 and 250 feet where the tufts are all large and up to 35 present per square yard. It occurs on rocks and also as an epiphyte upon *Sargassum*. Small *Padina* persist in the deeper part except between 504 and 600 feet. It becomes more abundant again as the moat merges on to the Boulder Tract (Graph 9), where algae other than a few greens do not occur. *Turbinaria*, unlike other algae, continues to increase as the moat deepens, and then suddenly becomes almost absent after 492 feet (Graph 10). A few specimens of *Digenea simplex* occur, and brown algae, other than *Padina*, are not found in the deeper part beyond 306 feet.

Among the green algae (Graph 7) *Anadyomene Brownii* resembles *Sargassum* in its distribution, and reaches its maximum in the shallower part, thereafter becoming scarcer and smaller (Graph 6). *Halimeda Opuntia* occurs on nearly every square yard in the shallower part, up to 24 large tufts being present on one square yard. *Boodlea paradoxa* is present on most square yards in the shallower part and almost disappears beyond 306 feet. *Dictyosphaeria favulosa* and allied species occurs occasionally up to 400 feet and then more rarely. *Bornetella nitida*, at first scarce, occurs occasionally except in the deepest parts, and becomes larger and more frequent between 200 and 240 feet. *Caulerpa*, represented mainly by *C. racemosa*, but sometimes by *C. sertularioides* and *C. cupressoides*, occurs on six square yards and is large in the middle of the shallower part. Green algae, except for small tufts of *Halimeda*, are absent from the deeper part, and towards the Boulder Tract species of *Dictyosphaeria*, *Boodlea paradoxa* and *Anadyomene Brownii* reappear in the shallow water.

Quantities of filamentous diatoms, such as *Biddulphia pulchella*, etc., occasionally form long tufts on the rocks and on living and dead corals.

Corals are few and small in pools in the shallower part, and increase to a maximum between 570 and 610 feet (see Graphs 2 and 3). This zone appears to lie beyond the deepest region, but where corals are thickest much dead coral debris accumulates on the sandy spaces between, so reducing the depth of water.

In the shallower part the bulk of the corals comprise massive *Porites* in small colonies 1-4 inches across and up to 15 in number on one square yard, *Leptastrea roissyana* 1-2 inches across and *Goniastrea pectinata* 1-4 inches across (see Graphs 19, 21 and 22).

In the deeper part *Montipora ramosa* becomes increasingly extensive. When the colonies reach the water surface their upward growth is checked beyond a maximum of 0.3 feet above the low-water level in the moat, and so flat-topped platforms are formed which rise highest in the middle of this region and may cover the whole width of the traverse (see level section and Plate IX). Only parts of the platforms are now living, as is shown by a comparison of graphs 16 and 17 of the distribution of platforms and living *M. ramosa*. Dead platforms are most extensive in the deepest parts. Outside the traverse *Acropora hebes* forms similar platforms (see also map of Acropore Moat, Plate X). Massive corals become progressively more extensive, and their upward growth is similarly checked, but at a slightly lower level; their tops die just above low-water level, forming flat platforms of some size with living vertical sides. The majority of platforms one square yard or more in area are formed by species of massive *Porites*, while species of *Favia** form smaller platforms rising to the same height. Massive *Porites* is fairly evenly distributed (Graph 19), and the size increases until platforms 10-30 inches across are formed. Beyond 600 feet only small knobs (1-3 inches) occur, although at about 640 feet large dead platforms are present. The levels of the platforms are given in the tables, p. 309.

Species of *Favia*, *Leptastrea*, etc., become most abundant between 560 and 610 feet, where available spaces are not covered by *M. ramosa* platforms (Graphs 16 and 20). Table I gives the species present, together with the numbers and sizes of the colonies. *Leptastrea roissyana* and *Goniastrea pectinata* become larger than in the shallower part, the former occurring more frequently (see Graphs 21 and 22). The Shoaling Moat near the Boulder Tract supports mainly *Favia* and *M. ramosa*.

Other corals occurring entirely or largely in the deepest parts of the Moat are *Pocillopora bulbosa* (1-8 inches), *Galaxea musicalis* (3-6 inches), *Psammocora gonagra* (1-10 inches), *Platygyra phrygia* (3-5 inches), species of *Acropora* (mainly *A. hebes*, *A. pulchra*, *A. quelchi* and *A. squamosa*), *Symphyllia* (3-8 inches), *Fungia*, *Cyphastrea* (2-7 inches), and *Coeloria* (see Graphs 25, 18, 29, 30, 28 and 26). They are found on dead faces of the massive coral platforms and on rocks between the extensive growth of *M. ramosa*.

A large-scale map of a portion of the Madrepor Moat is given in Plate X for comparison with the deeper part of the Western Moat, which is crossed by the survey (Plate IX). The bottom levels of the two moats in these positions are similar, lying at 2.1 feet and 2.0 feet above datum respectively. The physical conditions of the two regions show no marked differences, but there is more movement of sediment in the Madrepor Moat. However the corals and plants of these two regions are unlike; their growth, as seen in the mapped areas, appears to be of more recent date in the Madrepor Moat than in the Western Moat. The bottom of the Madrepor Moat is sandy, with little dead coral material

* Unless details of species are given the term "*Favia*" refers to *Favia* and other genera of closely similar external form, such as *Goniastrea*, *Leptastrea* and species of *Coeloria*, which are not conspicuously meandrine.

TABLE I.—*Species of Favia, Goniastrea, Leptastrea and Coeloria in the Moat on Traverse I.*

Coral.	Diameter of colonies in inches.	Numbers of colonies.
<i>Leptastrea roissyana</i>	1-12	105
<i>Goniastrea pectinata</i>	1-7	72
<i>Goniastrea retiformis</i>	1-12	73
<i>Favia favius</i>	1-9	65
<i>Favia abdita</i>	1-9	44
<i>Favia astraeiformis</i>	2-10	40
<i>Favia doreyensis</i>	1-6	23
<i>Coeloria daedalea</i>	2-9	20
<i>Favia K.18*</i>	2-7	18
<i>Favia halicora</i>	2-7	18
<i>Goniastrea</i> sp.	4	1
<i>Favia clouei</i>	5	1

Nearly half of the colonies of *Goniastrea* and *F. astraeiformis* occur between 564 and 600 feet and between 600 and 625 feet respectively, while almost all the *Coeloria daedalea* occur between 620 and 700 feet.

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.

on the surface, either as debris or rock, which could form suitable surfaces of attachment for living corals. The corals present are mainly platforms of *M. ramosa* and *A. hebes*, both of large size and entirely living, and some massive *Porites* which have not yet reached the water surface and formed platforms with dead tops. The algae are fairly numerous and *Thalassia Hemprichii* is abundant in the sand. The map of the Western Moat in contrast shows abundant dead coral material forming a rocky substratum for the attachment of other corals, a much richer variety of corals and very few algae. It may be noted that on the survey of Low Isles made by H.M.S. "Penguin" in 1905 no definite moat is shown where the Madrepor Moat now is, although the Western Moat is shown on the plan. It is probable that the Madrepor Moat shows a young stage of the same formation seen in the Western Moat.

(3) *The Boulder Tract. 700-846 feet. <2.9 feet above datum.*

The Boulder Tract here gradually rises from 2.6 feet, reaching 2.9 feet above datum at 755 feet. Thereafter it slopes more steeply downwards to 0.4 feet above datum at 846 feet. The substratum is composed of coral rocks and fragments with finer material between them. The rocky surface is fairly regular up to the crest, but beyond it irregular blocks of rock become larger and more frequent and may project 1.6 feet above the general level (see level section). The boring clam *Tridacna crocea* occurs in increasing abundance in these rocks (Graph 40). Gravelly sand lodges between the larger slabs of rock from 700 to 724 feet, and thereafter loose coral debris, such as composes the ramparts, lies over and among the rocks. Beyond 800 feet sand appears between the boulders, and water is held up in the small hollows.

A thin growth of microphytic algae is generally present, becoming thicker in the damper regions beyond 830 feet. Other algae are very small and limited to the lower or damper parts, being most frequent near the moat and scarce towards the Seaward Slope (see Graph 1). Isolated specimens of the red algae *Laurencia papillosa* (Graph 12), *L. obtusa*, *Galaxaura lapidescens* and *Amansia glomerata* occur towards the Seaward Slope. Small stunted *Padina* (Graph 9), and green algae (Graph 7) such as *Boodlea paradoxa*, *Dictyosphaeria favulosa* and other species and isolated specimens of *Bornetella nitida* and *Halimeda Opuntia* are found only on the slope towards the Moat. Blue-green algae, such as *Lyngbya majuscula*, are abundant locally on the damper parts of the Seaward Slope.

Corals are absent from the dryer parts of the Boulder Tract and appear again towards the Seaward Slope beyond 800 feet, small colonies of massive *Porites* and a few species of *Acropora* and *Favia* being present. At about 830 feet the rocks dip below low-water level, and corals then begin to increase (see level section and Graphs 2 and 3). *A. hebes* (Graph 31) is the dominant acropore at this upper limit of coral growth, but as the water deepens *A. squamosa*, *A. gemmifera* and *A. quelchi* make their appearance (Graphs 33 and 35), and also *Favia astraeiformis*, *F. favus* and *Goniastrea retiformis*.

Alcyonaria here make their first appearance (Graph 39) with two small colonies of *Sinularia polydactyla* and one of *Lobophytum crassum*.

(4) *The Seaward Slope. 846-1045 feet. <16.8 feet below datum.*

The reef slopes downwards here a little more steeply to a depth of 8.5 feet below datum at 1014 feet. Then follows a steeper slope descending to 16.8 feet below datum at 1045 feet. These two parts of the slope will be considered separately. The steeper slope drops downward at about 1 in 4.3 at first, and then at a slope of 1 in 9. Large coral heads projecting upwards 8 feet or more are only borne on the landward part of the slope up to 1014 feet, and the steeper part of the slope appears to coincide with the seaward limit of coral heads outside the traverse.

(a) *Landward Part of the Seaward Slope.*—The surface is composed of low coral rocks with occasional large boulders, the tops of which rise almost to low-water level and bear luxuriant coral growth forming "coral heads". The faces of such coral heads often slope downwards gradually towards the boulder tract and precipitously on their seaward faces (see boulder at 915 to 918 feet on level section). Between the low flat rocks and coral heads at 846 to 921 feet lie some clean sandy gaps. From 922 to 963 feet the rocky bottom becomes extremely rough. No sandy patches occur, and the rock surface is fairly clean. Uneven rocks then continue from 963 to 1014 feet with a large coral head at 1009 to 1014 feet, and others lying on either side of the traverse. A little blackish sand here appears between the boulders and a thin layer of grey mud lies on the rock surfaces.

Algae of any size are absent from this region onwards. Microphytic forms grow on the higher rocks which are not mud-covered, and otherwise only one small *Polysiphonia* was found (Graph 1).

The outstanding feature of this zone is the abundant coral growth on the higher parts of the slope and on the coral heads. Alcyonaria also become numerous (Graph 39). The numbers of species and of colonies of corals here reach their maxima for the traverse (see Graphs 2 and 3). The rocks are well covered by living coral up to 921 feet, and beyond more bare rock surface is present. The increasing depth enables a luxuriant growth of

projecting brackets of coral to be formed on the sides of the rocks, one above another, and bush-like growths to invade the sandy pools, while the upper parts of the larger boulders are densely covered (see large-scale map on Plate XI, *a*). The peaks on the graphs coincide with the larger coral heads seen in the level section. The region of greatest coral growth and of most numerous species per square yard of available space lies about 2 feet below datum.

Species of *Acropora* rapidly increase to a maximum between 846 and 890 feet (Graph 30), where each is found in a variety of positions, and shows no tendency to make platforms or other growth forms at definite levels as in the moat. A zoning of the more abundant species is apparent down the slope, as is indicated in Table II and Graphs 31–35. Other species less frequent in occurrence are *A. variabilis*, *A. hyacinthus*, *A. rosaria* and *A. formosa*. They are found mostly in the shallower water to 890 feet, but the last two also extend into deeper water to 976 feet. From 921 feet Acropores become few, and beyond 976 feet are practically absent.

TABLE II.—*The more Abundant Species of Acropora on the Seaward Slope of Traverse I.*

Species.	Level of maximum growth.	Remarks.
<i>A. hebes</i> . . .	0·8 ft. above datum .	Does not occur beyond 828 feet.
<i>A. gemmifera</i> . . .	0·4–1·2 ft. below datum .	Not very abundant.
<i>A. polymorpha</i> . . .	1·2 ft. „ „ .	Forms extensive growths of 1 sq. yd. or more, the tops lying at various levels. It does not extend to deeper water.
<i>A. squamosa</i> . . .	1·2 ft. „ „ .	Abundant, forming brackets and platforms 3–18 inches across.
<i>A. exilis</i> . . .	1·6 ft. „ „ .	The most abundant species as measured by the number of separate colonies. It forms bush-like growths 3–12 inches across.
<i>A. quelchi</i>	2 ft. „ „ .	Gradually increases in size as the water deepens to this level, and forms flat-topped brackets 2–18 inches across. It is also present near the surface on the large coral heads.

Favia, *Leptastrea*, etc., become increasingly abundant in number and species as the water deepens, and cover the rock surfaces not overgrown by Acropores (Graphs 20 and 30). They are particularly numerous on the larger boulders and coral heads (Plate XI, *a* and level section), but apart from these situations they are not so abundant as in the Moat, and become fewer and smaller in the deeper parts. Table III shows the species present, together with the numbers and sizes of the colonies and some remarks on their individual distribution. Of the two species common in the shallower part of the Moat, *Leptastrea roissigana* (Graph 21) is present, while *Goniastrea pectinata* does not here occur at all (Graph 22). *Goniastrea* K. 18,* present in the Moat, is here absent; other species found

* This coral could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.

in the Moat are either more or less frequent in different parts of the Seaward Slope, while *Favia vasta* and *Favia clouei* appear only on the deeper parts of the Seaward Slope (Graphs 24 and 23).

TABLE III.—*Species of Favia, Leptastrea, Goniastrea and Coeloria on the Seaward Slope of Traverse I.*

Species.	Size of colonies in inches.	Numbers of colonies.					Remarks.
		846–888 ft.	888–930 ft.	930–972 ft.	972–1014 ft.	1014–1045 ft.	
<i>Leptastrea roissyana</i>	1–6	0	7	3	1	0	Scarcely occurs in the richest coral zone, but extends to the deeper parts, much as it does into the shallower part of the Moat.
<i>Goniastrea retiformis</i>	1–16	10	9	5	2	1	} As in the Moat, these are most numerous species, but they here attain a larger size.
<i>Favia abdita</i>	1–7	4	5	4	4	0	
<i>Favia astraeiformis</i>	2–12	2	9	9	3	0	
<i>Favia favius</i>	2–7	3	10	10	10	1	
							Is more frequent than in the Moat and here persists into deeper parts as small colonies.
<i>Goniastrea</i> sp. K. 5*	2–10	7	4	0	4	0	Scarce in the Moat, but here more frequent in the shallower parts.
<i>Favia halicora</i>	3–8	2	6	4	2	0	Generally distributed here as in the Moat.
<i>Favia doreyensis</i>	2–6	4	2	2	4	0	Less frequent than in the Moat, and here larger in the shallower parts.
<i>Coeloria daedalea</i>	3–7	4	2	2	0	0	Does not extend to deeper water.
<i>Leptastrea ehrenbergiana</i>	2–7	2	0	2	0	0	Scarce.
<i>Favia</i> sp.†	4–6	0	2	0	1	0	Scarce; appears to be a deeper water form.
<i>Favia vasta</i>	3–7	0	0	3	4	0	} Become more frequent in deeper water, but are absent elsewhere.
<i>Favia clouei</i>	2–12	0	2	9	9	1	

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.

† These specimens have not been satisfactorily determined, and have been referred to either *F. Hemprichii* or *F. hirsuta* by Prof. Matthai.

Massive *Porites*, at first scarce and small, becomes more numerous in the richest coral zone, reaching 12 inches across, and is present occasionally throughout this section (Graph 19).

Of the other corals present in the Moat, *Psammocora gonagra* does not appear on the Seaward Slope (Graph 18). *Pocillopora bulbosa* occurs in scattered colonies (2–12 inches), but beyond 420 feet in the deeper water is replaced by *P. danae* (Graph 25). *Cyphastrea chalcidicum* (3–6 inches, Graph 26), *Symphyllia* (3–12 inches, Graph 28), *Coeloria* sps. and *Platygyra phrygia* occur mainly between 860 and 960 feet, and are more frequent and larger than in the Moat. *Montipora* (Graph 27) is abundant between 860 and 920 feet. It is mainly represented by encrusting growth forms from which arise fan and pillar-shaped upgrowths which may cover several square yards. *Galaxea musicalis* (3–7 inches) beyond 886 feet becomes large and abundant, and after 945 feet the large polyped *G. fascicularis* is usual (Graph 29).

Corals making their first appearance on the traverse are *Lobophyllia* sp. (2-12 inches), *Stylophora pistillata* (Esper) (6-12 inches) and *Astreopora* sp. (3-7 inches), see (Graphs 36-38; with occasional *Hydnophora* sp., *Heliopora*, *Merulina ampliata*, *Favia acropora*, *Turbinaria* sp., *Echinopora lamellosa* and *Millepora* sp. In the deeper parts *Echinopora gemmacea* is present; while *Pavona cactus* occurs occasionally in the shallower regions (*Pavona*, *Hydnophora*, *Echinopora*, *Lobophyllia* and *Merulina* are occasional in the Moat outside the traverse).

As the Seaward Slope deepens, the appearance of mud lying on the rocks in increasing thickness coincides with the reduction and final disappearance of *Acropora*, *Favia* and *Montipora*. In the deeper parts the dominant corals are *Stylophora*, *Lobophyllia*, *Astreopora* and *Galaxea fascicularis*, with a few *Echinopora gemmacea*, *Favia favius*, *F. vasta*, *F. clouei*, and the branching "*Porites Queenslandiae duodecima*" of Bernard.

The maximum growth of the Aleyonaria coincides with that of the corals (see Graphs 39 and 3). The following forms occur, but their distribution shows no marked zonation: *Lobophytum crassum*, *Simularia polydactyla*, *Lobularia pachyclados* and *Simularia lochmodes*. The Zoanthid *Palythoa* is here found occasionally.

The large-scale map on Plate XII shows the corals and Aleyonaria situated on the vertical face of a coral head lying off the N.E. corner of Low Isles. The position of the coral head is shown in Text-fig. 2b, "X". This coral head is just covered at low water springs, and the bottom round it is composed of clean coral debris containing little mud. The coral heads on and around the landward part of the Seaward Slope of Traverse I show similar coral growth upon their sides, but owing to the muddy bottom their bases are more barren; and since their tops are at a higher level, their upper parts bear a more abundant growth of Acropores. It may also be noted that although the rock surface is not completely covered, there is a greater variety in the species of coral present compared with those found on the shallower and more densely covered rocks seen in Plate XI, a.

(b) *The Steeper Part of the Seaward Slope*.—Beyond the coral head at 1009 to 1014 feet, the gentle slope becomes steep for a short distance (see level section and p. 279). A few boulders are present, but no more large coral heads, and the rocky bottom becomes less uneven. On this steep slope few fragments of coral rock lie on the rough surface, which is covered by a thick layer of easily disturbed mud.

Algae large enough to be detected from a diving helmet are absent.

Corals are now very few and small, and most are of massive growth form. They are situated mainly on the steeper rock faces and comprise the types found on the deeper parts of the landward part of the slope, *Astreopora* (2-8 inches) and massive *Porites*, often of large size (30 inches), being the most frequent (Graphs 38 and 19).

Acropora, *Montipora* and *Pocillopora* are absent. *Favia* are few, and *Galaxea* is almost restricted to the landward part of the slope (see Graphs 30, 27, 25, 20 and 29). Small specimens of the following are also present: *Lobophyllia* (2-8 inches), *Goniopora* (2-3 inches), *Turbinaria* (2 inches), *Stylophora pistillata* (3-6 inches), encrusting *Millepora* (3 inches) and *Merulina ampliata* (4 inches) (see Graphs 36 and 37). The mud lying on the rocks appears most unfavourable to corals, which apart from *Goniopora*, *Turbinaria* and *Stylophora pistillata* form small encrusting colonies, the tops of which may only just reach the surface level of the mud. The corals are clean but their edges may be dead, and they appear to be on the verge of being smothered by the mud.

A few Aleyonaria are present, mainly *Simularia flexibilis* and *Lobularia* sp.

(5) *The Sea Floor.* 1045–1089 feet. < 18·6 feet below datum.

The muddy sea floor is here reached, the even bottom sloping gently downwards. A little coral debris lies on the mud, and a few small rocks and two living boulders of massive *Porites* (30 inches) are present. Other corals and Alcyonaria are almost absent. Two *Astreopora* (16–20 inches, Graph 38) and single colonies of *Turbinaria* (3 inches), *Merulina ampliata* (3 inches), *Coeloria* (6 inches), *Sarcophyton trocheliophorum* (7 inches) and *Lobularia* sp. (6 inches) occur on the *Porites* boulders and small rocks (Graph 39). The mud is practically devoid of surface life. One large *Polyphyllia talpina* 34 × 7 cm. and some orange-coloured starfish (*Iconaster longimanus*) lie on the mud, and one clump of the alga *Digenea simplex* is present. The presence of the free fungiid *Polyphyllia* on the mud is remarkable, as this heavy coral must be successfully climbing upwards, with its cilia in continual movement, so counteracting its tendency to sink in the soft mud. The whole colony was in perfect condition, and showed no basal dead region as do most of the fixed corals. (See also the ability of *Fungia* to climb through sediment, Marshall and Orr, Vol. I, No. 5.)

Beyond 1045 feet the muddy sea floor appears devoid of rocks, corals and Alcyonaria, and the survey was discontinued after 1089 feet.

THE SURVEY OF TRAVERSE II.

The strip of reef examined along this traverse passes from the beach of the sand cay in a north-easterly direction across the reef (Luana reef, see Text-fig. 1), to end on a comparatively bare sandy stretch of bottom. A level section along the traverse is given with the graphs showing the distribution of organisms. The depth of water lying over the whole of the traverse varies directly with the state of the tide.

The traverse may conveniently be divided into the following portions for subsequent consideration: (1) *Beach Sand*, 0–52 feet, extending from the cay seawards, descends steeply from 12 to 5·5 feet above datum at a slope of 1 in 8. The sand is loose and devoid of corals and algae. (2) *Beach Sand-rock* ("beach rock" on Text-fig. 1) follows from 52 to 162 feet. Flat slabs of rock slope downwards to 1·4 feet above datum, and the rock is then broken away between 110 and 136 feet (see Text-fig. 1, and "m. 1." on level section). A narrow part of the Northern Moat lies just beyond the Sand Rock ("m. 2" on level section), and merges into (3) *The Inshore Part of the Reef*, an almost level area considerably overgrown by coral. It extends from 171 to 302 feet, sloping slightly from 1·2 to 0·8 feet above datum. Thereafter the downward slope increases over (4) *The Seaward Slope* from 302 to 500 feet, until the flat sandy bottom is reached at 5·2 feet below datum. This slope presents many irregularities in the form of masses of coral rock or living coral, so obscuring its true level, which is only revealed by the bottom levels of the sandy pools and the gaps between the irregular rocks (see level section, Plate V).

This traverse may be compared with that portion of Survey I which passes seawards from the Boulder Tract. The main differences between the two are correlated with the differences in profile, that of Survey I descending to about 18 feet below datum, while that of Survey II slopes gently to about 5½ feet below datum in about the same horizontal distance.

PHYSICAL CONDITIONS ALONG TRAVERSE II.

The physical conditions here show less variety than along Traverse I, and mainly resemble those existing on the *Seaward Slope* of the latter. The reef lies in protected water (see Text-fig. 1), except occasionally during the summer; the influences of moving water must be here at a minimum for Low Isles, and breakers are usually absent. The extremes of water level are indicated in the level section. At low spring tides the level Inshore Part of the reef dries out for a short time, but such tides only expose the tops of the higher rocks along the Seaward Slope. During low neap tides, when the reef is not fully exposed, the water remains shallow over the Inshore Part for considerable periods. Here conditions are at times obtained which may approach those prevailing in the Western Moat, but over a substratum at about 0·8 instead of about 2 feet above datum, and in a position open to deeper water instead of shut off from it. The Northern Moat ("m. 2.") at the point where the section crosses it is so narrow that it merges into the level Inshore Part of the reef both in its physical conditions and in the corals which it supports.

The diurnal variations in temperature, salinity and chemical composition of the water (see Orr, Vol. II, No. 4, p. 92 of these reports) are much smaller than on the Reef Flat, but are still considerable, and contrast with the deeper outside water beyond growing coral where such variations do not obtain. Seasonal variations are also less extreme than on the Reef Flat, and approach those present in the outside waters. The rate of deposition of sediment on the sandy stretch at the end of this traverse was usually less than in the Western Moat (see Marshall and Orr), and much finer in grain. No mud is present on the bottom on any part of this traverse, possibly owing to the small depth of the reef; and sediment probably does not here constitute a limiting factor for coral growth.

DETAILED ACCOUNT OF THE SUBSTRATUM, CORALS AND ALGAE OF TRAVERSE II.

The general remarks made for Traverse I (pp. 281–2) respecting the interpretation of the graphs and the season at which the survey was made are also applicable here. The peaks on the graph showing the distribution of coral colonies are less uneven than those on Traverse I, owing to the absence of large Coral Heads and extensive vertical faces of rock available for coral growth. Few *Hippopus* shells upon which corals and algae can become attached are present.

(1) *The Beach Sand.* 0–52 feet. 12–5·5 feet above datum.

Needs no further comment.

(2) *The Beach Sand-rock.* 52–110 feet and 136–162 feet. 5·5–1·4 feet above datum.

The rock here is smooth, flat and shelving. At first the slabs may lie at different levels, but all slope downwards at about 1 in 15. Beyond 107 feet the rock breaks up somewhat and sand appears upon it. The isolated patch of rock at 136–162 feet is much broken up by vertical cracks into flat slabs. These rocks are exposed for long periods at low water, and support a covering of slimy microphytic algae and a few rock oysters.

Where the rocks dip down to the arms of the Northern Moat ("m. 1." and "m. 2." on level section), a few red, brown and green algae appear (Graphs 41 and 46). Between 94 and 110 feet small *Padina* form the bulk of the few algae (see Graph 47); *Amphiroa fragilissima*, tufts of filamentous diatoms and some blue-green algae also occur.

Between 110 and 136 feet the rock is broken away, leaving a sandy area sinking to 0.8 feet above datum (see Text-fig. 1, and level section "m. 1."). Except at extremely low tides this is a sandy pool connected with the Northern Moat, and a few rock fragments lie freely on the sand. Algae are few and small, but more varied than on the beach sand-rock (see Graph 41). The submerged rocks bear a thicker covering of microphytic algae than those which are exposed, and filamentous diatoms are everywhere present. Green algae, represented by *Bornetella nitida*, appear in the middle of the pool (Graph 46). The brown algae are most frequent at the sides. *Padina* is the commonest (Graph 47), but *Colpomenia* and *Hydroclathrus clathratus* are also present as small isolated specimens. Red algae, such as *Galaxaura lapidescens*, *Amphiroa fragilissima*, *Laurencia papillosa* (Graph 48) and *Roschera glomerulata* occur in all parts of the pool, but are isolated and small in size. Two colonies 2 inches across of *Favia astraeiformis* and *Pocillopora bulbosa* are present (Graphs 52 and 53). A narrow arm of the Northern Moat ("m. 2." on level section), sinking to 0.4 feet above datum, lies between the beach sand-rock and 171 feet. The bottom is sandy, with few rocks and fragments. The corals and algae here resemble those of the following section, with which they will be considered.

(3) *The Inshore Part of the Reef. 171–302 feet. 1.2–0.8 feet above datum.*

Beyond the Moat the Inshore Part of the reef rises to about 1.2 feet above datum. The outstanding feature here is the growth of flat-topped platforms of branching coral, such as are seen in the Western Moat, and which here rise to 1.6 feet above datum (see level section). Seawards from the Moat the reef gently descends to about 0.8 feet above datum, where the coral platforms become more scanty. Finally the level drops abruptly to datum during the last 12 feet. The bottom, where not covered by coral platforms, is mainly sandy, with flat rocks and fragments in places. Only two *Hippopus* are present.

Unlike the Western Moat, very little *Thalassia Hemprichii* occurs in the sand between the coral platforms (Graph 45), and *Halophila ovalis* is absent.

The number of species of algae rises in the arm of the moat and decreases again when the coral platforms are most extensive. The maximum flora, both in variety and bulk, lies in the middle of this region where coral growth is smallest (see Graphs 41 and 42). The green algae are fairly evenly distributed (Graph 46). *Halimeda Opuntia* is present on every square yard and is often abundant, but becomes less extensive towards the Seaward Slope. *Halimeda macroloba* and species of *Dictyosphaeria* are fairly frequent, and *Bornetella nitida* becomes most numerous in the middle of this region. *Boodlea paradoxa*, *Caulerpa racemosa*, *C. sertularioides* and *C. cupressoides* are scarce, appearing two or three times. Brown algae are represented mainly by *Padina*, which becomes increasingly abundant as the *M. ramosa* platforms decrease, and then disappears suddenly beyond 286 feet (Graph 47). *Hydroclathrus clathratus* and *Digenea simplex* are occasional. The red algae are few. *Galaxaura* shows the same type of distribution as *Padina* (Graph 47). *Laurencia papillosa* and *Acanthophora spicifera* are not abundant (Graphs 48 and 49). *Gracilaria Textorii* and *Amphiroa fragilissima* are scarce and small, and *Galaxaura marginata* and *Amansia glomerulata* occur once or twice.

Filamentous diatoms are frequent, forming hair-like tufts.

The total number of coral species present per square yard increases fairly steadily along this section (Graph 43). The flat-topped platforms are entirely composed of branching corals, and, unlike those of the Western Moat, are almost all living. *Montipora ramosa* is the most extensive form, invading the Northern Moat and almost completely covering parts of the Inshore Reef to the exclusion of other coral and algal growth (Graph 50). *Acropora hebes* may also give small areas of platform (Graph 59). Other corals are at first few, some small *Leptastrea roissyana*, *Favia astraeiformis*, *Goniastrea* sp., *Cyphastrea chalcidicum* (1–4 inches) and one *Montipora foliosa* appearing (Graph 55). After 269 feet *Favias*, etc., become larger and more varied (Graph 52), being represented by *Goniastrea pectinata*, *F. favius*, *G. retiformis* (1–6 inches), *Goniastrea* K.18 * and in addition one *Pocillopora bulbosa*. As the reef slopes down to datum level large colonies of *A. pulchra* are found forming bush-like growths, their tops rising to about 2 feet above datum (see Graph 60, and level section). No other Acropores are present.

Alcyonaria appear on the Inshore reef, but reach their maximum abundance just beyond it (Graph 44). *Xenia* is seen first, growing in gaps between the coral platforms where pools of water lie except at lowest tides. Beyond 270 feet *Simularia polydactyla* covers areas up to 18 inches across, large *Sarcophyton trocheliophorum* and *S. glaucum* are frequent, and a few *Lobophytum crassum* occur.

(4) *The Seaward Slope.* 302–500 feet. 0–5·2 feet below datum.

The slope descends at a gradient of about 1 in 52, its seaward edge dropping more steeply to the flat sandy floor of the anchorage. The slope is mainly covered by extensive patches of loose coral rock, very uneven and full of holes and caverns. Larger gaps between these rocks form sandy pools which may be partially overgrown by corals projecting into them from the rocks. Three such pools are crossed by the traverse, (1) from 304 to 334 feet, (2) from 354 to 362 feet, and (3) from 406 to 430 feet, the bottom levels in the three being 0·8, 1·4 and 2·4 feet below datum respectively.

Algae are few from the first, and apart from microphytic forms on the rocks, rapidly become absent along the traverse. Up to 347 feet *Galaxaura lapidescens*, *Gracilaria Textorii*, *Roschera glomerulata*, *Bornetella nitida*, species of *Dictyosphaeria*, *Halimeda Opuntia* and *H. macroloba* are present (Graphs 41 and 46).

Filamentous diatoms are present everywhere, forming large tufts on the rocks and corals.

Coral growth over the Seaward Slope is rich, and increases in numbers and variety up to the limit of the reef. The abundance of bare irregular coral rocks which project upwards to just above datum level now restricts most of the living coral to the sides and crevices of the rocks and to the tops of rocks situated well below datum level. The higher rocks are either bare, or covered by encrusting and other corals which have been partially or completely killed at times, and have recolonized these situations while conditions remained favourable. Plate XI, *b* shows a map of part of the traverse at about 366 feet. Rocks rise from pool 2 (see above) to about datum level, or just above it, and are very richly covered by living coral.

* This coral could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.

From 302 to 364 feet the corals are composed of forms found already on the Inshore Part of the Reef and in the Western Moat, but with a greater number of species of *Acropora* (see Graph 58). Corals are mainly represented by *Montipora ramosa* (Graph 50), *M. foliosa*, species of *Favia* (Graphs 52 and 55), and Acropores. *M. ramosa* forms fairly extensive platforms over the higher rocks, but much is dead and is then covered in part by Alcyonaria. Unlike the Acropores, *M. ramosa* does not spread into the deeper pools. Beyond 364 feet the rocks are very thickly covered by living coral (see Plate XI, *b*). *M. ramosa* is absent, but Acropores and encrusting species of *Montipora* abound, and may be of more brittle build than those nearer the shore. New genera make their appearance, while species of *Favia* are fewer and smaller.

Species of *Favia*, *Goniastrea*, etc., are most abundant up to 360 feet, and grow on the ledges, vertical faces and hollows of the rocks. They are almost as numerous as on the Seaward Slope of Traverse I, and the relative frequency of occurrence of the species is much as it is on the shallower parts of the latter situation. Species found in the deeper parts of Traverse I do not occur. Table IV gives the species present together with notes on their distribution.

TABLE IV.—*Species of Favia, Leptastrea, Goniastrea and Coeloria on the Seaward Slope of Traverse II.*

Species.	Diameter of colonies in inches.	Numbers of colonies.		Remarks.
		302-364 ft.	364-500 ft.	
<i>Leptastrea roissiana</i>	3-4	2	1	Occurs here and on the inshore part of the reef, as it does on the reef flat and Seaward Slope of Traverse I.
<i>Goniastrea retiformis</i>	2-10	16	8	The largest and most numerous species, as on the Seaward Slope of Traverse I.
<i>Favia abdita</i>	3-7	6	2	} Frequent, as on Seaward Slope of Traverse I.
<i>Favia astraeiformis</i>	2-6	7	1	
<i>Favia favius</i>	2-6	4	6	
<i>Goniastrea K. 5*</i>	4-6	4	0	Frequent, as on Seaward Slope of Traverse I.
<i>Favia halicora</i>	2-6	12	0	More frequent than on Seaward Slope of Traverse I.
<i>Favia doreyensis</i>	2-8	5	1	Frequent, as on Seaward Slope of Traverse I.
<i>Coeloria</i> sp.	2-5	1	5	..
<i>Goniastrea solida</i>	3	0	1	..

Goniastrea pectinata, present of the inshore part of the reef and on the reef flat of Traverse I, is here absent, as on the Seaward Slope of Traverse I.

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.

Montipora foliosa and *M. erythraea* become increasingly frequent up to 430 feet (Graph 55), the colonies covering areas up to 24 inches across. They appear in all situations, but chiefly as a horizontal covering of the higher rocks, from which turret-like and foliose projections grow where space permits.

The Acropores are abundant in both species and colonies, forming a few high platforms which are partly dead, and bush- and bracket-like growths projecting into the pools.

Table V shows the species and colonies present, and the distribution of some of them is shown in Graphs 58–65, for comparison with Traverse I (Graphs 30–35). *Acropora hebes* is almost restricted to the inshore part of the reef (Graph 59); it also characterizes the higher parts of the Seaward Slope of Traverse I. *Acropora pulchra* (Graph 60) is characteristic of parts of the traverse just above datum which are directly open to deeper water; and *Acropora rosaria* (Graph 65) is present in the deeper parts much as on Traverse I. No marked zoning in the distribution of other Acropores is perceptible, possibly owing to the gentle slope of this region, and the abundance of rock near the surface of the sea.

TABLE V.—*Species of Acropora present on the Seaward Slope of Traverse II.*

Species.	Diameter of colonies in inches.	Numbers of colonies.		Remarks.
		302–364 ft.	364–500 ft.	
<i>A. hebes</i>		7 sq. ft.	0	Almost restricted to the inshore part of the Reef.
<i>A. pulchra</i>		7 sq. ft.	0	Grows on rocks in the middle of Pool 1, but does not appear again.
<i>A. gemmifera</i>		2 sq. ft., 1 colony	4 sq. ft. 2 (colonies 6 inches)	Not abundant, but fairly frequent in the shallower parts and on the higher rocks.
<i>A. polymorpha</i>		1 sq. ft.	31 sq. ft., 9 (colonies 6–14 inches)	..
<i>A. delicatula</i>	3–18	4 colonies	18 colonies	..
<i>A. formosa</i>	2–8	3	5	..
<i>A. quelchi</i>	2–15	3	44	..
<i>A. squamosa</i>	3–18	1	17	..
<i>A. rosaria</i>	3–12	1	6	..
<i>A. exilis</i>	3–24	0	70	Particularly abundant at the seaward edge of the reef.
<i>A. loripes</i>	3–7	0	5	..

Massive *Porites*, previously appearing but once, becomes more frequent (Graph 51), but the colonies are small in size (1–7 inches).

As on the Inshore Part of the Reef, a few small *Pocillopora bulbosa* and *Cyphastrea* occur, but not beyond 376 feet (Graphs 53 and 54). *Galaxea* of increasing size (<10 inches) and numbers and *Symphyllia* are most frequent on the landward part of the Seaward Slope, and one *Coeloria* is present (Graphs 56 and 57). Beyond 364 feet *Seriatopora hystrix*, massive *Porites* sps. and *Fungia* (Graphs 68, 51 and 71) appear. The latter become numerous on the edge of the reef lying among the rocks and covered by undisturbed water. *Stylophora pistillata*, *Lobophyllia*, *Heliopora* (Graphs 66, 67 and 70), *Psammocora exesa*, of a massive growth form, *Echinopora lamellosa*, another coarser species of *Echinopora* and *Platygyra phrygia* occur infrequently, and outside the traverse an occasional *Goniastrea* and *Turbinaria* occur (see Plate XI, b).

The seaward edge of the reef is characterized here by an extensive and fragile growth of *Acropora exilis*, *A. rosaria*, and by large and delicate expansions of *Montipora foliosa*, together with abundant *Fungia* extending down to the sandy bottom beyond the reef (Graphs 63, 65, 55 and 71). On either side of the traverse living corals of the reef edge project upwards and outwards, forming an almost vertical wall composed of *Acropora hyacinthus*, *A. rosaria* and *A. exilis*, with occasional large bush-like colonies of *Heliopora*.

The flat sandy bottom beyond the reef edge from 480 to 500 feet is almost devoid of corals, two small colonies of *A. exilis* and a few of *A. polymorpha* being attached to rocks in the sand.

Alcyonaria (Graph 44) become larger and more abundant on the Seaward Slope of Luana reef than on any other part of Low Isles. They flourish most in the shallower pools near the level inshore part of the reef and on rock surfaces which are usually just submerged. The richest alcyonarian pools lie to one side of the traverse, and a portion of such a pool is mapped in Plate XIII. Further out the alcyonaria may be very large, although not so numerous, and occur mainly on the rocks just below datum.

Xenia, present on the Inshore Part of the Reef, only occurs again as small colonies in pool I between 302 and 312 feet. *Nephtya mollis* is found in abundance at about 314 feet growing on dead coral, and covers one square yard of debris on the sand beyond the reef edge. *Clavularia inflata* var. *luzoniana* appears on the traverse at the edge of the reef, covering 8 square feet between 444 and 455 feet, but is also found in the richest alcyonarian pools to one side of the traverse. Other Alcyonaria present are shown in Table VI. The most frequent are *Sarcophyton trocheliophorum* and *S. glaucum*, often very large, and usually growing in positions which just expose the colonies at low spring tide, and *Alcyonium pachyclados*, occurring abundantly as small isolated colonies 1-6 inches across or in extensive masses 2 feet across.

TABLE VI.—*Alcyonaria, other than Xenia, Nephtya and Clavularia, present on the Seaward Slope of Traverse II.*

Species.	Diameter of colonies in inches.	Numbers of colonies.
<i>Alcyonium pachyclados</i> . . .	4-24 .	34
<i>Sarcophyton trocheliophorum</i> . . .	2-30 .	13
<i>Simularia polydactyla</i> . . .	4-18 .	14
<i>Lobophytum crassum</i> . . .	4-9 .	4
<i>Lobophytum pauciflorum</i> var. <i>validum</i>	4-28 .	3
<i>Simularia lochmodes</i> . . .	3 .	1

Other Alcyonaria not encountered on the traverse but present just outside it are *Simularia flexibilis* and other species (see Plate XIII). These and *Clavularia inflata* var. *luzoniana* are not exposed at low spring tides, whereas *Sarcophyton trocheliophorum*, *Simularia polydactyla*, *Lobophytum crassum*, *Lithophytum arboreum* and *Xenia* may be completely exposed.

The Zoanthid *Palythoa* is found on the most exposed rocks of the traverse beyond 400 feet, 5 colonies (<10 inches) being present.

On Plate XIII are mapped two areas in the rich alcyonarian zone on the lee side of the reef near Traverse II. The bottom lies at about 1 foot below datum. A few sandy pools lie in this region, as seen in Map A, but where the substratum is rocky, alcyonarian growth may be almost continuous, as seen on the left side of Map A. This region may be compared with the rich coral zones on the seaward slope (1) at 2 feet below datum on Traverse I (Plate XI, b), and (2) at 1.4 feet below datum on Traverse II (Plate XI, b).

THE SURVEY OF TRAVERSE III.

The position of this Traverse is seen in Text-fig. 1, and it is shortly referred to in Vol. III, No. 2, p. 64 of these reports. It passes from the outer rampart over the windward edge of the reef in line with the lighthouse and E. beacon in a south-easterly direction. A level section along this traverse is given, the vertical and horizontal scales being the same as used for the seaward slopes of traverses I and II, so that direct comparisons may be made. It is apparent that this windward side of the reef descends in a short distance to a much greater depth than does the leeward side. The former drops to 86 feet below datum at 1155 feet from the crest of the outer rampart, while the latter at 850 feet from the crest of the boulder tract becomes nearly level at a depth of 36 feet (see level section of Traverse I and Text-fig. 1). The Seaward Slope of Traverse III at first descends with about the same steepness as on the leeward side (Traverse I), but it continues so for a greater distance until a depth of 20 feet below datum is reached at 877 feet. Here the reef drops almost precipitously to a depth of 48 feet at 945 feet, and then less steeply down to 86 feet. Beyond this deep the sea floor shoals to 78 feet below datum. The traverse first crosses the inner rampart, composed of "honeycomb" rock (0-74 feet), and then passes over the outer rampart covered by shingle (74-298 feet). Honeycomb rock then becomes exposed, as shown in the map (Text-fig. 1), and continues to about 580 feet. Small boulders rise 2-4 feet from the general level, which further out is composed of rocks and sandy patches. Sand continues beyond 680 feet. From 867 feet outwards the nature of the substratum could not be observed from a boat. No mud is present here in the shallow water as occurs on the lee side of the reef (Traverse I). A detailed survey of the organisms living along this traverse would be desirable for comparison with those on Traverses I and II on the leeward side; however, owing to lack of available time and calm weather which would permit the use of a diving helmet, such a survey was impossible. By means of a boat and water telescope the dominant organisms were noted on the traverse down to about 16 feet below datum. For this purpose the upper part of the seaward slope was divided into four 100-foot regions, and the organisms occurring on each are recorded below the level section (Plate VIII). As would be expected, algae only occur on the upper part of the slope just below datum, and are few in numbers and species, as on the other seaward slopes of Low Isles.

The corals form a luxuriantly growing belt which extends into much deeper water than on the lee side of the reef. At a depth of 16 feet and below, as far as could be seen from a boat, *Montiporas* and *Acroporas* abound, forming huge colonies, whereas on Traverse I corals had become very few at this depth, and were absent at 18 feet where the muddy lagoon floor was reached.

The corals occurring on the first 100 feet of the Seaward Slope (see level section) resemble those present on the leeward side of the reef (see Seaward Slope, Traverse I), with the addition of large and small massive species of *Pocillopora* (*P. verrucosa* and *P. eydouxi*) and *Acropora decipiens*. These corals do not occur elsewhere on Low Isles, and are characteristic of the exposed outer ridge and reef crest of outer barrier reefs such as Yonge Reef.

On the second 100 feet of the traverse where small boulders rise to low-water level many corals seen on the previous section persist, such as *A. squamosa*, *G. retiformis*, *F. doreyensis*, *Millepora*, etc., but others which characterize shallow water elsewhere on

Low Isles do not occur again, such as *F. abdita*, *F. halicora*, *Hydnophora*, *Platygyra*, *Pocillopora bulbosa*, etc. The Outer Barrier Reef forms noted above continue, and to them are added others such as *A. abrotanoides*, a coarse growth form of *A. gemmifera* (also seen on Yonge Reef), and *A. hyacinthus* and others of that type.

On the third 100 feet of the slope the shallow-water *Favias* and *Pocilloporas* are absent. The deeper-water *Favias* of Traverse I continue or appear for the first time, such as *F. clouei*, *F. vasta* and *F. favius*. Deeper-water forms found also on the lee side appear, such as *P. danae*, *Stylophora*, *Lobophyllia*, *Seriatopora* and *Heliopora*, make their appearance. Of the outer barrier reef "Outer Ridge" forms, *A. decipiens*, *A. gemmifera*, *A. abrotanoides* and *Pocillopora eydouxi* do not continue into this deeper water. *Millepora* forms very large branching colonies and *Montiporas* give huge fan and bracket-like growths.

On the fourth 100 feet the *Acroporas* are luxuriant and mostly resemble outer barrier reef types. *A. polymorpha* shows many coarse growth forms, and *A. hyacinthus*, etc., occur as large flat or dish-like brackets. Stag-horn types become very large and tree-like. Other corals identifiable from a boat are luxuriant, such as large *Montiporas*, branching *Millepora*, and *Favia favius* and *Leptastrea ehrenbergana*. This list is not to be considered in any way exhaustive, but it represents the larger and more conspicuous forms.

Beyond 860 feet the corals on the Seaward Slope could not be identified from a boat, and the record thus ends.

DISCUSSION AND CONCLUSIONS.

Some of the points of interest arising out of the surveys may now be considered.

Algae occur in abundance only along parts of Traverse I, and are almost absent on the Seaward Slopes of all three traverses. In the Western Moat and on the Inshore Part of Traverse II the abundance of algal species is approximately inversely proportional to the numbers of species of corals. All the major groups of algae are at a maximum in the shallower part of the Moat, where temperature and other extremes are greatest. They are fewer on the reef flat and are practically absent outside the Boulder Tract, even where corals are scarce and the water shallow. They decrease in numbers towards the drying flat and in the deeper water of the Moat.

The limiting factors for this algal distribution are not readily apparent, although corals are doubtless absent from the shallower parts of the Moat owing to the extremes of the physical conditions. The shallower Moat differs from its deeper parts in the wider extremes of temperature and salinity, while the oxygen content may remain stationary, or even fall at the end of a low-tide period instead of increasing to supersaturation. The pH rises during the day in all parts of the Moat, but CO₂ does not appear to be a limiting factor for plant growth. Possibly nutrient salts are of more importance. Phosphate determinations by Orr indicate that decomposition takes place in the reef flat sand at a short distance below the surface. Undisturbed sand contains an appreciable quantity of soluble phosphates, but Moat sand, which is being continually moved about and washed, contains little. At low tide the deeper Moat water seldom contains recognizable traces of phosphates. However, corals are able to utilize phosphates (Yonge, Vol. I, No. 6, p. 150), and presumably other salts, directly from the water both during the day and

night, so that less phosphates, etc., must be available for algae in the deeper Moat where corals grow.

The brown algae are fewer than the reds and greens, and the green algae comprise most of the widely distributed species, which extend to all parts of the Moat and Boulder Tract. On the Dry Tortugas, Taylor finds a somewhat similar type of algal distribution. In the moat of Garden Key the stagnant water covers a flora mainly composed of red and green algae; while the bathymetric distribution of algae shows that the reds, browns and greens all decrease below 3 metres, but the greens become dominant in deeper water (70–90 metres). Taylor considers the distribution to be primarily dependant upon light, and the red algae in deeper water to be inhibited by the soft character of the bottom. On Low Isles along Traverse I light cannot be the main factor in the distribution of red, brown and green algae, since all parts of the Moat and the upper part of the Seaward Slope are well illuminated; neither can the soft mud on the Seaward Slope be responsible for the absence of algae here, since mud is only present in the deeper parts.

The different positions of maximum growth of the more important algae can be compared in graphs 6–15. Most species show a gradual rise and fall about their maxima, but *Anadyomene Brownii* and *Sargassum* suddenly reach their maxima in the shallower water and gradually fall off in the deeper Moat (Graphs 6 and 8), while *Turbinaria* (Graph 10) shows the inverse type of distribution, gradually rising to a maximum as the Moat deepens and then suddenly falling off before reaching the deepest parts.

The distribution of corals along the traverses is not likely to be influenced by the supply of plankton and the variations in oxygen content, the pH and the excess base of the water. It probably depends principally upon factors such as the levels of the substratum relative to that of low water, the ranges of temperature, salinity, etc., of the water, and the nature and amount of sediments which are deposited and which may lie undisturbed on the rocks and corals.

The maximum coral growth (Graph 3) occurs in the deeper parts of the Moat, and on the Seaward Slope of Traverse I at about 2 feet below datum. (The possible cause of the reduction of corals below this level here will be considered below.) The greater part of the reef along Traverse II is little more than 2 feet below datum, and corals steadily increase in numbers to the reef edge (Graph 43); the rise in numbers of corals beyond 416 feet at the seaward edge, where the depth is at first little increased, perhaps may be associated with the more direct exposure of this region to open water at extreme low tides. On Traverse III coral growth continues luxuriantly below 16 feet.

The level of the zones bearing the greatest numbers of species and of colonies coincide on both Traverses I and II (Graphs 2, 3, 42 and 43). On the fringing reef off the windward side of Maer Island and on the Aua reef, Tutuila, Mayor found the greatest number of coral species close behind the outer edge of the reef, while the maximum numbers of colonies occurred some distance from the edge (400 feet on Maer Island). It must be remembered that these reefs contrast in form and position with Low Isles, and the coral bearing surface of their flats is very much wider than any of the rich coral zones traversed by the Low Isles survey.

The upper limit of coral growth is determined in the first place by the range of water level. In the Moat the height of the branched and massive coral platforms appears to be controlled by the permanent level of low water, and lies at 0.3 and 0.15 feet respectively above the latter. Outside the Boulder Tract and rampart coral growth starts at a lower

level, just above datum (see Traverses I and III), so that corals are only exposed to the air intermittently at exceptionally low tides. No platforms are here formed with flat dead or living tops at a constant level since the water is continually changing, but over the level inshore part of Traverse II coral growth, except for *Acropora hebes*, is checked above 1.6 feet above datum (see level sections).

Massive corals with flat dead tops have been noted in other regions by Darwin, Semper and Wood Jones. The cause of the dead tops has been ascribed by Darwin and Semper to tide level and consequent exposure to air, sun and rain, while Wood Jones considers that on Cocos Keeling atoll the majority of cases are due to the deposition and accumulation of sediment in amounts greater than can be removed by normal agencies. The distribution of such dead-topped corals on the traverses and on Low Isles generally, where they are found abundantly in Moats but rarely outside the Boulder Tract, even in regions where sediment is the limiting factor, and the direct correlation of the height of such colonies with low-water level, indicates that here water level and not sediment is the main factor responsible for such growth forms on Low Isles.

The distribution of various corals is clearly influenced by their several abilities to withstand heat and silt. Thus *Acroporas* which easily succumb to silt and heat (Mayer, 1924) occur mainly on the upper parts of the Seaward Slope of Traverse I and over a large part of Traverse III, but are infrequent in the Moat and absent in muddy zones such as the deeper parts of Traverse I; while massive *Porites*, well able to withstand silt and heat (Mayer, 1924), is present at all levels on the traverses wherever there is water (Graphs 19, 51, 30 and 58).

The Moat provides the greatest extremes of temperature, exposure, etc., on the reef. During the summer, high temperatures may cause a considerable mortality, and the winter night minimum may be too cool for reef corals, which are injured by a temperature below about 18.5° C. (Mayer, 1924). The presence of rich coral growth in the Moat may be made possible by the occurrence of semi-diurnal tides, which gives a maximum exposure of only 5½ hours. Movement of sediment is considerable in the Moat, but corals here are well able to remove the coarse sandy sediment from their surfaces by their own activity and by the aid of water movements. The dominant Moat coral is *Montipora ramosa* (Graph 16), and it is restricted to this type of region. In the shallow moats of similar form on the reefs in the Bay of Batavia *M. ramosa* may be almost the only coral present, and even this may be absent if there is no cooling circulation of water through the moat. The temperatures here are not more extreme, but the moats may be exposed for 12 hours as there is only a single tide a day.

Among the Moat corals some appear extremely resistant to exposure or to a wide range of conditions. *Pocillopora bulbosa* (Graph 25) occurs in the Western Moat and through most of the Seaward Slope of Traverse I. Massive *Porites* has been mentioned above, and among the species of *Favia*, etc., *Goniastrea pectinata* and *Leptastrea roissyana* are the only corals other than massive *Porites* which can live in the shallow as well as the deeper parts of the Moat. *Leptastrea roissyana* (Graph 21) occurs throughout the Seaward Slope also, and is almost as successful as massive *Porites* in living under a wide range of conditions. Others appear to thrive in the deeper part only of the Moat, and grow equally well on the shallower part of the Seaward Slope; such are *Cyphastrea* and many species of *Favia* (Graphs 20 and 26). Corals such as *Acropora*, *Galaxea*, *Symphyllia* and *Montipora foliosa* in the Moat are restricted to the deeper parts and reach their

maximum growth on the Seaward Slopes (Graphs 30, 29 and 28); they usually do not live in the more exposed moats of the reefs in the Bay of Batavia.

On Traverse II the gentle slope of the Inshore Part of the Reef results in conditions prevailing for part of the year which approach those of the Western Moat to a certain extent. A resemblance between the corals and algae of the two regions is present, although the Moat lies at 1·8–2·4 feet with its *M. ramosa* platform at 2·8 feet above datum, while the Inshore Part of the reef on Traverse II lies at 0·8–1·2 feet, with its *M. ramosa* platform at 1·6 feet above datum. Differences between the two regions, however, exist. On Traverse II all the *M. ramosa* is living, massive *Porites* is scarce and *Psammocora* absent (Graphs 50 and 51). The algae, although various (Graphs 46–49), are far less abundant, the phanerogams almost absent (Graph 45), and filamentous diatoms are much more abundant than in the Western Moat.

For details of the effects of various types of sediment on corals on Low Isles, reference should be made to Marshall and Orr, Vol. I, No. 5 of these reports. Corals can remove considerable quantities of coarse sand and fine mud which may fall upon them, either by muscular or ciliary activity, or by entangling the finest mud in mucus, which is then swept away. In the removal of sediment corals may be aided considerably by water currents. The ability of different species to remove sediment varies, but usually sediment does not appear to be directly harmful to growing corals unless they are actually buried by it.

Some of the effects of sediment can clearly be seen by a comparison of the three traverses. On the Seaward Slopes the reduced range of temperature and the constant circulation of water of nearly uniform composition permits the growth of a much richer coral fauna than elsewhere. Forms appearing exceptionally in the Moat here reach a maximum and many new types occur. Coral growth on Traverse I, however, is strongly inhibited at a small distance below datum, although light, food, range of temperature and free circulation of water can hardly be very different at so slight a depth. Yet on other reefs coral growth is luxuriant down to several fathoms, and on Traverse III across the windward edge corals are luxuriant far below 16 feet. The limiting factor on the leeward edge appears to be mainly the deposition of fine grey mud, which lies undisturbed on all surfaces in increasing thickness down the Seaward Slope. Mud is found in appreciable thickness from about 4 feet below datum on Traverse I, and corals diminish here in numbers and size directly as the mud increases (see level section and Graph 3). On the windward side of Low Isles the rocks are clean as far down as could be seen from a boat, and coral growth persists into deeper water.

The fine grey sediment on the leeward side appears to be more harmful than the coarse sandy sediment falling in the Moat, but the exact nature of its effects upon growing coral is not clear. Since the sediment lies thickly on exposed rocks, corals must be dependent mainly upon their own activity rather than on water currents for its removal. Small corals may here be liable to be smothered by muddy sediment, which is much more easily shifted by water currents than is sand, but once it has covered the coral, is not more easily removed by the coral itself. The smothering of a coral by mud, when this takes place, appears to act by removal of aerated water, which leads to suffocation. The fine sediment does not itself appear to be necessarily poisonous. The deleterious effect of grey mud has been pointed out in other regions by Gardiner (1930, pp. 4–9).

It has been shown (Marshall and Orr) that large-polyped corals can deal with sediment

falling from above more effectively than some of the small-polyped forms. Thus *Fungia*, *Galaxea*, *Symphyllia* and *Goniastrea pectinata* all readily remove large amounts of mud and sand falling on them, while massive *Porites* only removes mud easily, and *Psammocora* is unable to remove much fine sediment. It is noteworthy that on Traverse I *Psammocora* does not appear on the Seaward Slope, where mud lies on the rocks, but is present on clean vertical faces of coral heads (Plate XII) outside the Traverse; and that as the deeper muddier regions are reached, the majority of corals able to withstand these conditions have large polyps. The deeper water *Favia vasta*, *F. clouei*, *Astreopora* and *Lobophyllia* have larger polyps than the species found in shallow water. Massive *Porites*, however, according to Marshall and Orr appears to be least efficient at removing sediment, especially if it is coarse, yet it is found all along the Traverse, and its surface is clean down to the muddiest regions where corals grow.

The associations of corals on the Seaward Slope of the lee side of the reef are roughly of three types. In the shallower water, where the deleterious influence of the mud is not felt, Acroporas are dominant, and *Favia*, *Symphyllia* and *Cyphastrea* are numerous (Graphs 30, 20, 28 and 26). Some of the acroporas show a zoning correlated with depth (Graphs 31-35). Throughout the rest of the Seaward Slope where the influence of the mud begins, many *Favia*, *Pocillopora*, *Montipora*, *Galaxea*, *Stylophora*, *Astreopora* and *Lobophyllia* occur (Graphs 20, 25, 27, 36, 38 and 37). In deeper muddier regions only a few *Stylophora*, *Lobophyllia*, *Astreopora*, *Favia clouei*, *F. vasta*, *F. favus* and branching *Porites* can live besides the widely distributed massive *Porites*.

A zoning of the corals on the Seaward Slope of Traverse II is less marked than on Traverse I, as a depth of only 5.2 feet below datum is reached and mud is not present. The most marked zoning is that of the acroporas in shallow water, which resembles that on Traverse I. The gentle slope here allows the abundant growth of *Acropora pulchra* (Graph 60) at 0-0.4 feet above datum, which only appears at this level occasionally on the steeper parts of the N.W. side of Low Isles. The abundance of Fungidae (Graph 71) on the Seaward part of Traverse II may be correlated with the comparatively undisturbed water. They are absent from the outer parts of Traverse I, but are present in the quiet water of the *Fungia* Moat. Species of *Favia* (Graph 52), on the other hand, are less numerous than on Traverse I (Graph 20), where they appear to withstand more mud than the acroporas, and thus can extend further seawards. On Traverse II the numbers of *Favia* and *Acropora* colonies are roughly inversely proportional (Graphs 52 and 58), and on the outer half of the Seaward Slope where the acroporas are abundant the *Favias* are few or absent.

The fauna of the Seaward Slope of Traverse III presents several noteworthy features. It does not include corals which characterize the moats, but which also occur in small numbers on the Seaward Slopes of the lee side of the reef, such as *Leptastrea roissiana*. It comprises very many forms characteristic of the other Seaward Slopes, such as those recorded for Traverse I; and in the deeper parts of Traverse III stag-horn types are found such as also grow in the Anchorage of Low Isles, and in the Anchorage Coral Zone on the lee side of Outer Barrier Reefs. On this exposed windward corner of Low Isles is found the nearest approach to the conditions prevailing on the Outer Barrier Reefs, and it is here only on Low Isles that many corals are found which characterize the outer parts and crests of such reefs. The most noteworthy forms are Acroporas such as *A. abrotanoides* and *A. decipiens*, and other species which occur elsewhere but here show stout

and coarse growth forms such as *A. gemmifera* and *A. polymorpha*. These are all very resistant to wave action. In deeper water below 16 feet the huge stag-horn growths of *Acropora* and the fans of *Montipora* occur also in the deeper parts of the Low Isles Anchorage and on the less exposed parts of Outer Barrier Reefs at similar or greater depths.

There is little indication as to how far distribution of corals may be influenced by competition between species for the available space. Mayor (1918) has suggested that such competition takes place on parts of the reef flat of Maer Island. On Traverse I, only in the *Acropora* zone of the Seaward Slope are corals so closely packed that the rocks are completely covered, and it is unlikely that where quick growing and extensive *Acroporas* are present other corals can easily become established in quantity. On Traverse II the distribution of *Favia* and *Acropora* may perhaps be taken as an example of effective competition between corals for the available space, *Acropora* crowding out the *Favia*. The sides of rocks and more low-lying sites for coral growth on the Seaward Slope are so densely clothed by coral that considerable competition between species must exist. However the tops of the rocks about datum level are regions where successful coral growth is determined by ability of the corals to withstand the limiting factors of both normal and exceptional physical conditions. On a narrow reef such as this, regions can be recognized where coral distribution is effected mainly by (1) direct reaction to the physical environment, or (2) competition between species, but the regions are not widely separated as Mayor describes on the fringing reefs of Tutuila and Maer Island.

Traverse II may be compared in its position with the short account by Hedley and Taylor (1907) of a traverse across the lee side of East Hope Isle, another "island reef" situated some 40 miles north of Low Isles. Here the living reef 40 feet wide is narrower and far less rich in varieties of coral. The edge of the reef is dominated by *Goniastrea* and *Porites*, with more delicate *Acropores* between them. Behind lies a zone of *Turbinaria*, *Coeloria*, *Fungia*, *Galaxea*, *Herpetolitha* and *Acropora*, and then two zones follow between the living coral and the sand cay; these are 100 and 200 yards wide and dominated by alcyonaria and algae respectively. The alcyonarian zone is far more extensive and luxurious than on Low Isles, *Sarcophyton* reaching 8 feet across. No level area dominated by *M. ramosa* occurs. The algal zone, which is richer than on Traverse II, extends from that of the alcyonaria to the beach. Details of levels along this traverse are not given.

On the traverse across a New Hebrides fringing reef, Baker (1925) describes an area largely covered by *M. ramosa* lying near the shore as on Traverse II. The level of this region is not given, but it appears to lie between 0 and 2.6 feet below datum. If this is so, then it is considerably lower than the Inshore Part of Traverse II, which is dominated by *M. ramosa*.

II. DESCRIPTION OF SMALL AREAS ILLUSTRATING THE CORAL FAUNA ON CHARACTERISTIC ZONES OF AN OUTER BARRIER REEF (YONGE REEF)

The several types of Island, Inner and Outer reefs occurring off the coast of Queensland have been described by Spender (1930), and their mutual differences noted. Ecological features of Island Reefs have been considered in the preceding section and in Vol. III, No. 2, and by Spender, 1930. Of the Outer reefs which we visited there was

reason to consider Yonge Reef to be an example showing very completely the basic type of Outer Barrier Reef (Spender, 1930, p. 31).

Plates XIV–XVI show large-scale maps of typical areas on an Outer Barrier Reef (Yonge Reef). Reference should be made to Mr. Spender's description, 'Geographical Journal', Vol. LXXVI, p. 32, and to Vol. III, No. 2, Text-fig. 5, and Plate XVII, fig. 2 of these reports, which illustrate the main features of an Outer Barrier Reef. No detailed quantitative work was done on the coral fauna of an Outer Barrier Reef; and as the data referring to such reefs is not presented together in any one part of these reports, the record of coral fauna on selected areas of an Outer Barrier Reef is included here, so that ready comparison may be made with the records of selected areas on Low Isles. The Pacific "Outer Ridge" could not be mapped owing to water conditions. The areas chosen lie on the "Reef Crest", the "Outer Moat", the "Anchorage Coral Zone" and the "Zone of Coral Heads".

The differences in physical conditions prevailing on Outer Barrier Reefs and Island Reefs are chiefly two, those of level, and of water composition and movements. The low level of outer reefs compared with other types of reefs off the Queensland coast has been discussed by Spender, 1930, p. 35, and a consideration of weather and water conditions and their biological significance around barrier reefs has been given by Orr, Vol. II, No. 3 of these reports, together with a comparison of conditions in other localities in the barrier reef region (pp. 60 and 66).

REEF CREST.

Plate XIV shows a small area on the Reef Crest, which extends over 3 miles in length and 100 yards in breadth, and forms the highest part of the reef. The reef crest is shortly described in Vol. III, No. 2, pp. 32 and 84, Text-fig. 5, and Plates XVII, fig. 2, and XXIII, figs. 1, 3 and 4, and by Spender, 1930, p. 83.

Much of the reef crest bears less living coral than this particular patch. A smooth and very hard substratum is formed by coral rock covered by a veneer of nullipores. None of the corals project far above the surface, and they are few in both numbers and species, leaving extensive areas of bare rock (compare Plates IX, XI and XIII, where little rock is not covered by corals).

The Acropores tend to show a pedestal-like growth, the upper fan or bush of branches being separated from the substratum by a narrow and solid "stem". This growth form is not apparent when viewed from above in the map. The acropores are also all strongly built, *A. gemmifera* (species 6 on map) showing a stouter growth form than occurs on Low Isles in sheltered water. *Tubipora* is a conspicuous feature of this area; the pink *Pocillopora verrucosa* is frequent; knob-like and encrusting corals are fairly numerous (*Millepora*, *Montipora*, etc.), but together with the *Favias*, are small in size. A grey Zoanthid and the sponge *Phyllospongia ridleyi* are characteristic features, and the bright green alga *Chlorodesmis comosa* and the starfish *Linkia guildingii* are conspicuous. Little dead material is present here, but may be more abundant in other parts. No loose debris lies on the surface of this high smooth rock.

The number of coral genera is small, and except for *Tubipora*, they represent types of very general occurrence on all types of reef. Of the 9 species of *Favia* (and allied genera), 3 occur also on the upper parts of the Seaward Slopes of both windward and

leeward sides of Low Isles, on the sides of coral heads, and in Moats of Low Isles (*Goniastrea retiformis*, *Favia abdita* and *Coeloria* sp.). They are thus able to exist under very variable conditions. Three others occur also on both the Seaward Slopes and on coral heads on Low Isles, but not in the moats (*Goniastrea* K. 5, *Leptastrea ehrenbergana*, *Favia clouei*), and can thus live in varied conditions, but the extremes prevailing in Moats appear to be more severe than on the Yonge Reef Crest. Of the remaining three species (*Favia laxa*, *F. waykayana* and one undetermined sp.), only one is recorded from Low Isles, and that from the side of a coral head, and they thus appear to favour more open water.

The Acropores present on the Reef Crest are also found on both Seaward Slopes of Low Isles, with the exception of *A. pulchra* and *A. rosaria*. It is noteworthy that *A. hebes*, occurring on Low Isles at higher levels than other acropores, is here found on the highest part of the reef.

OUTER MOAT.

Plate XV shows two areas in the Outer Moat region. This zone (see Vol. III, No. 2, pp. 32 and 83, and Spender, 1930, p. 32) is about 100 yards wide and lies between the reef crest and the outer ridge at the Pacific edge. It lies at a lower level than both Reef Crest and Outer Ridge, and is usually filled with water even at low tide, but the water is agitated and not still as in the Low Isles moats. The rock is heavily encrusted with nullipores, its surface is smooth and devoid of debris and loose material. Corals here are both varied and luxuriant, but do not project vertically to any great extent. Many more genera are present than on Low Isles moats (compare Plates IX and X), and many of the species here are distinct from those occurring on Low Isles.

Conspicuous corals seen on the map are the wide dish-like expansions of *Acropora hyacinthus*, etc. (12 on the map), the encrusting and knob-like upgrowths of *A. palifera*, coarse low-lying branches of *A. decipiens* (upper area), very stout colonies of *A. gemmifera* (6 on map), and small finely branching colonies of *A. delicatula* (13, lower area). The coarsely branching *Pocillopora verrucosa* grows larger than on the reef crest, while the very large *Pocillopora eydouxi* forms solid pink masses several feet long (lower area). Massive corals cover less area than do the branched ones (compare reef crest where massive corals are more numerous), but they may be very large in size (ex. *Coeloria*, upper area) and are usually without dead tops. The genera of massive form are very varied, being represented by *Coeloria*, *Platygyra*, *Hydnophora*, *Favia*, *Leptastrea*, *Goniastrea*, *Porites*, etc. No loose corals occur, such as *Fungia*. A few Alcyonaria are found, typically *Nephthya mollis* (upper area), various *Xenias*, and the curious nephthyid *Paralemnalia thyrsoides* mimicking an Acropore such as *A. quelchi*. The hydroid *Aglaophenia cupressina* and the sponge *Phyllospongia ridleyi* (upper area) are frequent.

This Moat contrasts in almost all its features with the Low Isles Moats, and has more in common with the inshore part (first 200 feet) of the Seaward Slope on the windward side of Low Isles (see Traverse III, level section) than with any other part of Low Isles reef. Here also occur the giant *P. eydouxi* (absent elsewhere on Low Isles and on the leeward side of Yonge Reef), *Leptastrea ehrenbergana* (present elsewhere on Low Isles on coral heads), the very large massive corals, and acropores such as *A. decipiens*, *A. abrotanoides*, and the stout variety of *A. gemmifera* (occurring nowhere else on Low Isles).

INNER PARTS OF THE REEF.

The leeward side of the reef from the Reef Crest passes through the Inner Moat to the Boulder Zone, and so to the Anchorage Coral Zone and Zone of Coral Heads (see Vol. III, No. 2, pp. 34 and 85, and Spender, 1930, p. 33). In the Anchorage Coral Zone the substratum changes from rock to rock intersected by sandy pools, the sandy floor sloping gradually from 1-2 feet to 2-3 fathoms below low water. The rock surface is much rougher and is less heavily covered by nullipores, and lies in boulders and uneven masses. The upper area on Plate XVI illustrates a typical portion of the Anchorage Coral Zone; the water here lies about 4 feet deep in the pools (see also Vol. III, No. 2, Plate XXIV, fig. b). The Anchorage Coral Zone passes gradually into that of Coral Heads, masses of coral rock rising precipitously from the sandy floor. These coral heads are several or many yards across, and their tops are covered with a rich growth of corals which may overhang at the edges. The edge of a coral head is mapped below on Plate XVI (see also Vol. III, No. 2, Plate XXIV, fig. 2). These zones show a preponderance of branching corals, particularly Acropores, and show a certain resemblance to the areas so named on Low Isles.

On the Anchorage Coral Zone on Yonge Reef (Plate XVI, upper area), *A. palifera* and both coarse and fine varieties of *A. gemmifera* are conspicuous on the higher parts, while large "stag-horn" acropores grow into the pools. Other noteworthy branching forms are *Seriatopora*, *Pocillopora verrucosa*, *P. danae* and *Stylophora*. It will be noticed that *A. gemmifera*, *A. palifera* and *P. verrucosa* also occur in the Outer Moat, but that unlike the Outer Moat, *P. eydouxi* is here absent. In the presence of Fungias, *Seriatopora*, *Stylophora*, *P. danae* and stag-horn acropores a resemblance is seen to the Low Isles Anchorage. The massive corals are various. They may be very large and grow so high as to show dead flat tops. *Goniastrea retiformis*, *Favia abdita*, *F. halicora* and *Goniastrea* K. 5* are very frequent; these are corals found in most situations on Low Isles and on Yonge Reef. Fungias and *F. fava* are more particular in habitat, and occur here and on coral heads and leeward slopes and moats of Low Isles, but are not frequent on other parts of Yonge Reef. *F. vasta*, found in the deeper parts of the Low Isles leeward slope, is also found on the Yonge Reef anchorage zone.

Coral Heads have already been described, Vol. II, No. 2, p. 85, and the map below on Plate XVI showing the edge viewed from above may be compared with the Low Isles coral heads viewed from the side (Plate XII, and Vol. III, No. 2, Plate XVII, fig. 1).

In conclusion, it may be said that the examination of the above areas, although not extensive, illustrates certain general features in comparison with Low Isles.

On the two reefs many similar corals occur, and the external appearance of most massive corals of the same species seems identical on the two reefs. With the branching corals, particularly the Acropores, such is not the case, and much greater variety of form is apparent among corals growing on different regions. A few are constant in external appearance in different localities, such as *A. decipiens*, coarse and fine forms of *A. gemmifera*, etc., but the appearance of others varies somewhat from one region to another, or they are replaced by slightly different varieties or growth forms in endless combinations.

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.

Until the relations of the varying growth forms and species of Acropores is elucidated, adequate description of coral associations becomes impossible.

On the two reefs certain corals seem to be very accommodating in their requirements, and are found in a great variety of habitats. Such are *Goniastrea retiformis*, *Favia abdita* and *F. halicora*, which occur alike in moats, leeward and windward slopes and edges of both reefs. Other corals are less accommodating, and occur mainly in certain habitats, such as leeward slopes and moats, ex. *F. vasta* and *Fungia*, or the windward slopes and outer regions, ex. *Pocillopora eydouxi* and *Acropora decipiens*, etc.

On the one reef a definite zonation in the distribution of the coral fauna may be clearly defined (as shown by distribution graphs for Low Isles). On Yonge Reef, where environmental conditions differ, the zonation of corals shows some similarities to that on Low Isles, but some differences. The region seaward from the reef crest on Yonge Reef resembles the windward slope of Low Isles in some of its physical features and in characteristic corals such as *P. eydouxi*, etc., and the leeward side of Yonge Reef also shows many features in common with the leeward slopes and anchorage of Low Isles. However, on Yonge Reef, but not on Low Isles, several corals characteristic of the seaward sides are found on the leeward side as well, such as the coarse variety of *A. gemmifera*; and corals such as *Stylophora*, *Seriatopora* and *F. vasta*, which occur on the leeward side of both reefs, are found in deeper water on the windward slope of Low Isles. This may indicate that the conditions for coral growth on the seaward slope of the windward side of Low Isles may be in some degree intermediate between those present on the leeward and seaward sides of Yonge Reef.

SUMMARY.

1. An account is given of a quantitative survey of the corals and algae present along a strip of reef one yard wide, made over two traverses across the lee side of Low Isles. The survey was continued down the seaward slopes of the reef by the use of a diving helmet. A less detailed account of a third traverse across the windward side of the reef is given.

2. Measurements of levels and distances and level sections along the traverses are given.

3. The main physical features along the traverses which may influence coral and algal growth are recorded.

4. Large-scale maps of limited areas illustrate the comparisons of different regions of the reef in detail, and serve as a record of the present state of certain parts of Low Isles reef.

5. The survey records details of the varieties and numbers of algae and corals on each square yard, passing through the stringent physical conditions prevailing in the Western Moat, and over the more luxuriant coral zones on the Seaward Slopes of the reef. The Traverses end (1) on the muddy sea floor, devoid of corals and algae, at about 20 feet below datum, and (2) on a barren sandy stretch of the floor of the Anchorage at 5.5 feet below datum. On Traverse III records are given of corals down to a depth of 16, but coral growth continues far below this level.

6. Algae are most abundant in the shallower parts of the Moat, and corals in the deeper part of the Moat and on the Seaward Slopes.

7. A zoning of the corals on the Seaward Slopes is shown. It is correlated in the first place with the levels of the substratum. On Traverse I the maximum growth of corals, in both numbers of species and of colonies, lies at about 2 feet below datum; on Traverse III luxuriant coral growth extends into much deeper water.

8. The environmental factors which are likely to influence coral and algal growth along the traverses are considered. The most important of these are probably (1) level of the substratum in relation to that of low water and to the maximum duration of low tides, (2) the ranges of temperature and salinity of the water, and (3) the nature and amount of the sediments which are deposited and which may lie undisturbed on rocks and corals.

9. Observations and records on Traverse I indicate that at slight depths the deposition of fine grey mud, which is not entirely removed from projecting surfaces by water movements, is unfavourable for corals, and here constitutes a limiting factor for coral growth.

10. This survey is briefly compared with existing detailed accounts of restricted areas on other reefs.

11. Large-scale maps are given of limited areas from typical zones of an Outer Barrier reef (Yonge Reef) for comparison with Low Isles.

REFERENCES.

- BAKER, J. R. 1925. A Coral Reef in the New Hebrides. *Proc. Zool. Soc. Lond.* 1925, pp. 1007-1019, 8 text-figs.
- GARDINER, J. S. 1930. Studies in Coral Reefs. *Bull. Mus. Comp. Zool. Harv.* LXXI, pp. 2-16.
- HEDLEY, C., and TAYLOR, T. G. 1907. Coral Reefs of the Great Barrier, Queensland: A Study of their Structure, Life-distribution, and Relation to Mainland Physiography. *Rep. Aust. Ass. Adv. Sci. Adelaide*, XI, pp. 397-413, pls. i-iii, 6 text-figs.
- MARSHALL, S. M., and ORR, A. P. 1931. Sedimentation on Low Isles Reef, and its Relation to Coral Growth. *Sci. Rep. Gt. Barrier Reef Exped. I*, pp. 93-133, pls. i-iii, 7 text-figs.
- MAYER, A. G. [= MAYOR]. 1918. Ecology of the Murray Island Coral Reef. *Pap. Dept. Mar. Biol. Carn. Inst. Washington*, IX, pp. 1-48, pls. i-xix, 9 text-figs.
- MAYOR, A. G. [= MAYER]. 1924. Structure and Ecology of Samoan Reefs. *Pap. Dept. Mar. Biol. Carn. Inst. Washington*, XIX, pp. 1-25, pls. i-viii, 4 text-figs.
- ORR, A. P. 1933. Physical and Chemical Conditions in the Sea in the Neighbourhood of the Great Barrier Reef. *Sci. Rep. Gt. Barrier Reef Exped. II*, pp. 37-86, 7 text-figs.
- and MOORHOUSE, F. W. 1933. (a) Variations in some Physical and Chemical Conditions on and near Low Isles Reef; (b) The Temperature of the Waters in the Anchorage, Low Isles. *Sci. Rep. Gt. Barrier Reef Exped. II*, pp. 87-101, 1 pl., text-figs. 1-3.
- SPENDER, M. A. 1930. Island Reefs of the Queensland Coast. *Geogr. J.* LVI, pp. 193-214, 273-297, illust.
- STEPHENSON, T. A., STEPHENSON, A., TANDY, G., and SPENDER, M. A. 1931. The Structure and Ecology of Low Isles and other Reefs. *Sci. Rep. Gt. Barrier Reef Exped. III*, pp. 17-112, pls. i-xxvii, 15 text-figs.
- TAYLOR, W. R. 1928. The Marine Algae of Florida with special reference to the Dry Tortugas. *Pap. Dept. Mar. Biol. Carn. Inst. Washington*, XXV, pp. 219, pls. i-xxxvii.
- WOOD-JONES, F. 1910. Coral and Atolls. Pp. xxiii, 392, pls. xxvii, 1 map, 1 port., 79 text-figs. London.

TABLES OF LEVELS ALONG THE TRAVERSES.

Levels along Traverse I. Distances are measured in feet from the beginning of the traverse on the Thalamita flat; see Text-fig. 1, and level section.

Distances.	Heights above or below datum in feet.		
0	.	2.79	
12	.	2.70	
25	.	2.71	
35	.	2.59	
50	.	2.51	
64	.	2.49	
74	.	2.55	
85	.	2.59	
100	.	2.54	
110	.	2.48	
120	.	2.43	
142	.	2.47	
155	.	2.39	
170	.	2.58	
185	.	2.45	
200	.	2.44	
215	.	2.45	
230	.	2.50	
247	.	2.40	
260	.	2.41	
273	.	2.54	
285	.	2.39	
289	.	2.92 ("platform" of <i>M. ramosa</i>).	
300	.	2.39	
315	.	2.50	
325	.	2.89	" "
335	.	2.31	
345	.	2.39	
352	.	2.95	" "
360	.	2.29	
375	.	2.41	
389	.	2.13	
397	.	2.94	" "
400	.	2.19	
410	.	2.22	
416	.	3.01	" "
417	.	2.86 (	" massive <i>Porites</i>).
427	.	2.15	
435	.	3.00 (	" <i>M. ramosa</i>).
441	.	2.34	
450	.	2.08	
455	.	3.00	" "
462	.	2.28	
467	.	3.00	" "
480	.	2.17	
493	.	2.14	
500	.	2.19	
516	.	1.87	
527	.	2.24	

Distances.	Heights above or below datum in feet.	
537	.	2.84 (" platform " of massive <i>Porites</i>).
538	.	2.73 (,, <i>M. ramosa</i>).
541	.	1.78
552	.	2.91 ,, "
560	.	1.90
570	.	2.28
577	.	2.99 ,, "
583	.	2.01
593	.	2.85 (,, massive <i>Porites</i>).
596	.	2.01
599	.	2.93 (,, <i>M. ramosa</i>).
615	.	2.83 (,, massive <i>Porites</i>).
617	.	2.56
630	.	1.96
643	.	2.05
650	.	2.87
664	.	2.35
674	.	2.41
689	.	2.37
698	.	2.60
699	.	2.76
710	.	2.86
730	.	2.97
755	.	2.98
771	.	1.98
780	.	2.13
790	.	1.55
800	.	0.88
815	.	0.65
832	.	-0.03
845	.	-0.14
852	.	-0.70
854	.	0.35 (,, <i>Acropora polymorpha</i>).
865	.	-1.24
868	.	0.26 (,, <i>Acroporas</i>).
880	.	0.11 (top of corals).
882	.	-1.12
892	.	-1.97
900	.	-2.05
910	.	-2.85
922	.	-0.05 (top of rock).
926	.	-3.50
929	.	-2.10 ,,
943	.	-4.60
960	.	-0.40 ,,
967	.	-6.60
981	.	-5.50
1000	.	-8.60 (base of rock 6 feet high).
1007	.	-8.50 (,, 7 ,,).
1027	.	-15.00
1045	.	-17.00
1059	.	-17.50
1085	.	-18.50
1089	.	-18.50

Levels along Traverse II. Distances are measured in feet from the beginning of the Traverse on the beach; see Text-fig. 1 and level sections.

Distances.	Heights above or below datum in feet.		
0	.	12.08	
35	.	8.26	
55	.	5.58	
77	.	4.18	
78	.	4.92	
100	.	3.44	
105	.	2.52	
120	.	1.43	
133	.	0.73	
134	.	1.43	
150	.	2.89	
159	.	3.06	(top of rocks).
165	.	1.20	
174	.	0.38	
178	.	1.50	("platform" of <i>M. ramosa</i>).
201	.	1.49	" "
216	.	1.46	" "
217	.	1.16	
230	.	1.60	" "
245	.	1.50	(" " and rocks).
251	.	1.16	
270	.	0.86	
282	.	0.90	
291	.	0.85	
295	.	2.06	(top of <i>A. hebes</i>).
299	.	0.54	
310	.	-0.19	
324	.	-0.65	
325	.	0.48	(" coral platform).
336	.	-0.81	
342	.	0.59	" " "
352	.	0.61	" " "
359	.	-1.38	
367	.	0.17	(" rocks and coral).
380	.	0.17	" " "
395	.	0.52	" " "
406	.	0.24	" " "
409	.	-2.21	
417	.	-0.12	" " "
422	.	-1.40	
425	.	-0.41	(" coral).
430	.	-2.49	
432	.	0.00	(rock and coral).
450	.	0.25	" "
460	.	-0.99	(top of coral).
470	.	-2.07	" "
476	.	-3.80	
482	.	-5.20	
488	.	-5.20	

Levels along Traverse III. Distances are measured in feet from the beginning of the traverse on the Inner Rampart; see Text-fig. 1, and level section.

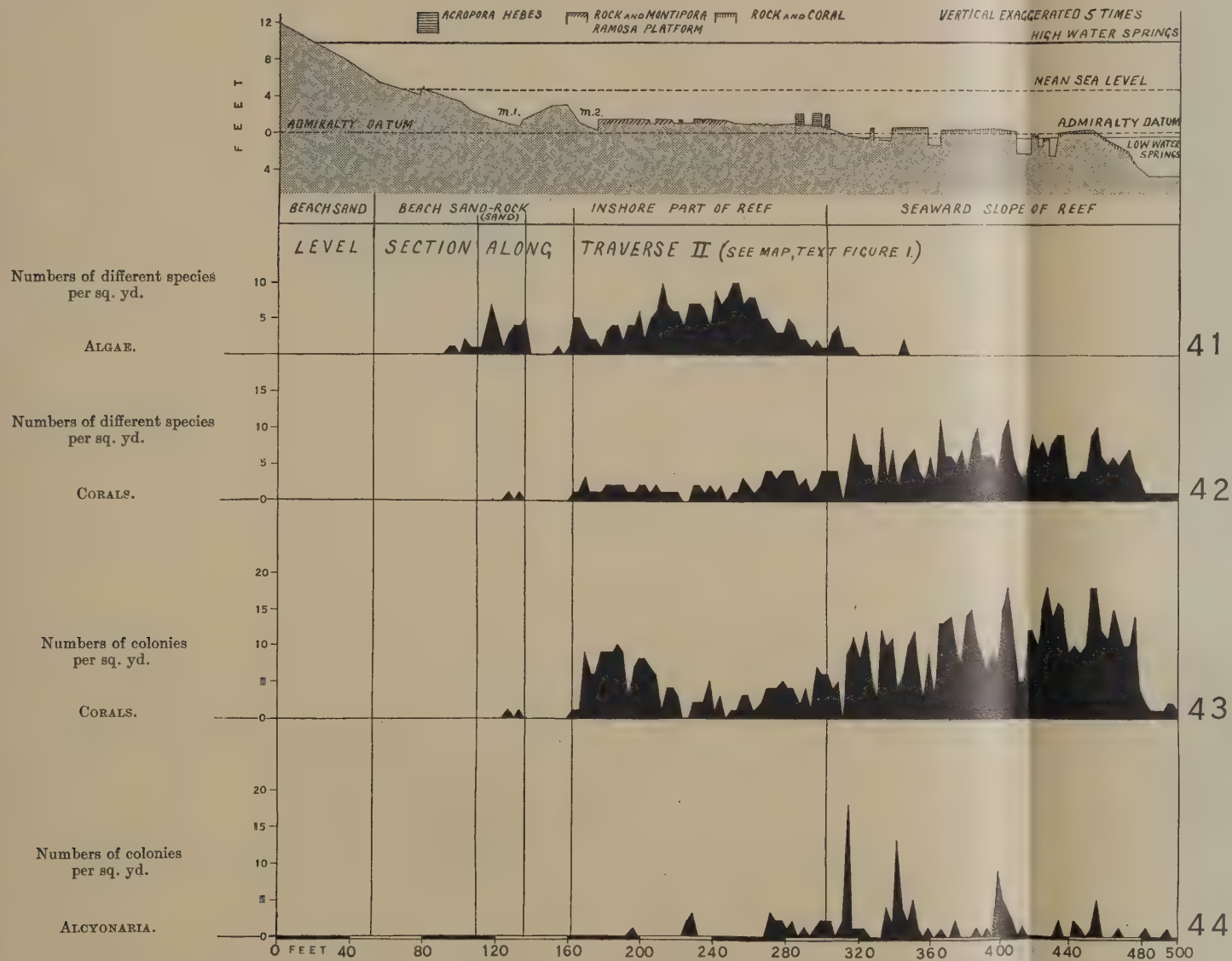
Distances.	Heights above or below datum in feet.	
0	.	5.49
62	.	4.56
75	.	7.45
268	.	3.27
300	.	2.53
350	.	2.03
415	.	0.97
460	.	0.14
480	.	-0.20
503	.	-0.70
520	.	-1.30
535	.	-1.40
560	.	-1.90
571	.	0.80 (top of rock).
577	.	-2.00
588	.	-3.50
606	.	0.20 " "
619	.	-4.20
628	.	-0.40 " "
643	.	-4.40
652	.	-5.20
679	.	-8.00
703	.	-8.00
721	.	-9.00
735	.	-10.00
744	.	-10.00
763	.	-10.00
783	.	-12.00
807	.	-16.00
835	.	-16.00
867	.	-16.00
877	.	-20.00
906	.	-21.00
923	.	-29.00
941	.	-44.00
945	.	-48.00
964	.	-51.00
991	.	-57.00
1051	.	-65.00
1075	.	-74.00
1155	.	-86.00

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).

REPORTS, VOL. III, No. 10.

PLATE V.



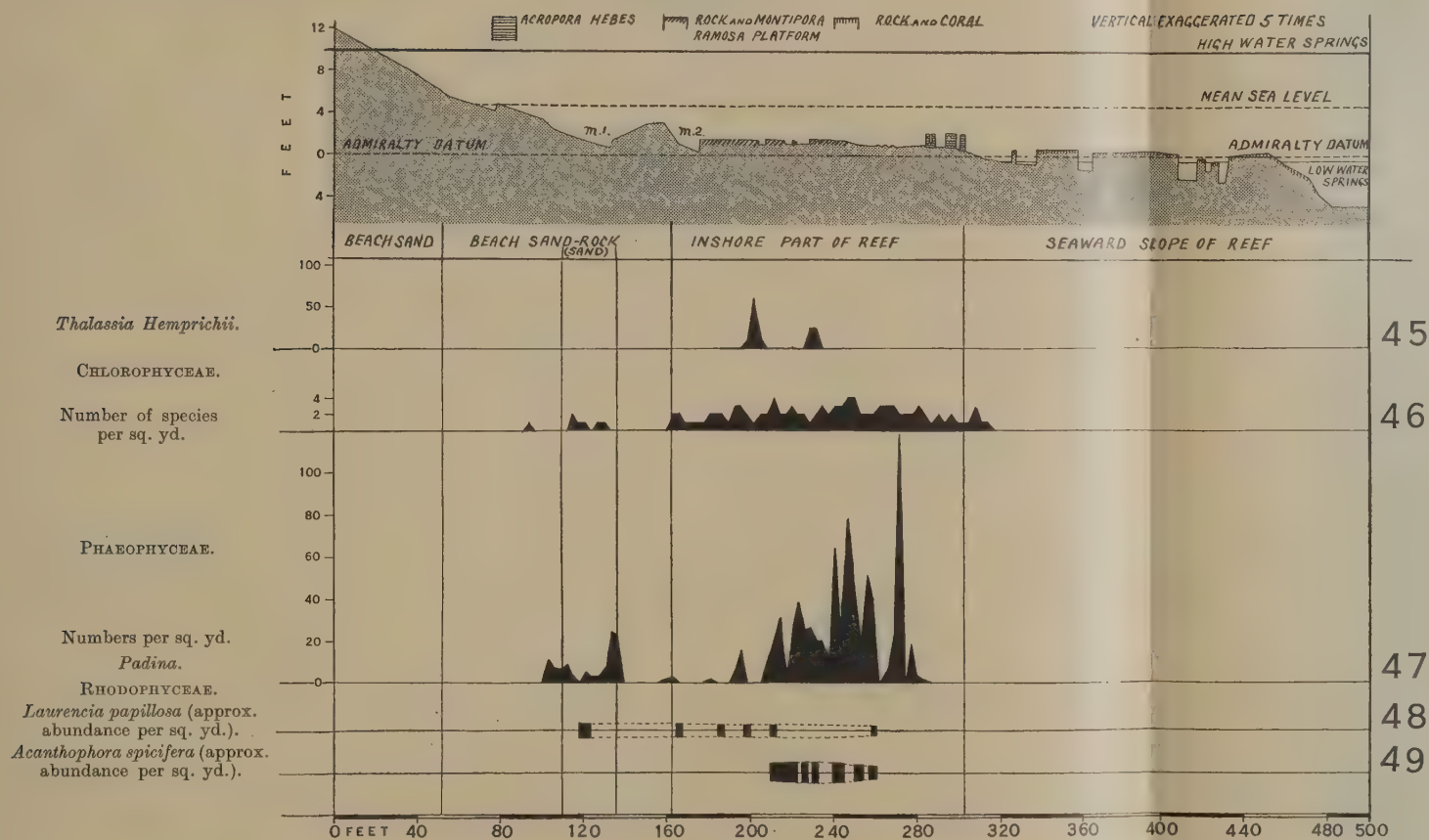
TRAVERSE II.—Distribution of Algae, Corals and Alcyonaria. Total numbers of colonies and species.

GREAT BARRIER REEF EXPEDITION 1928-29.

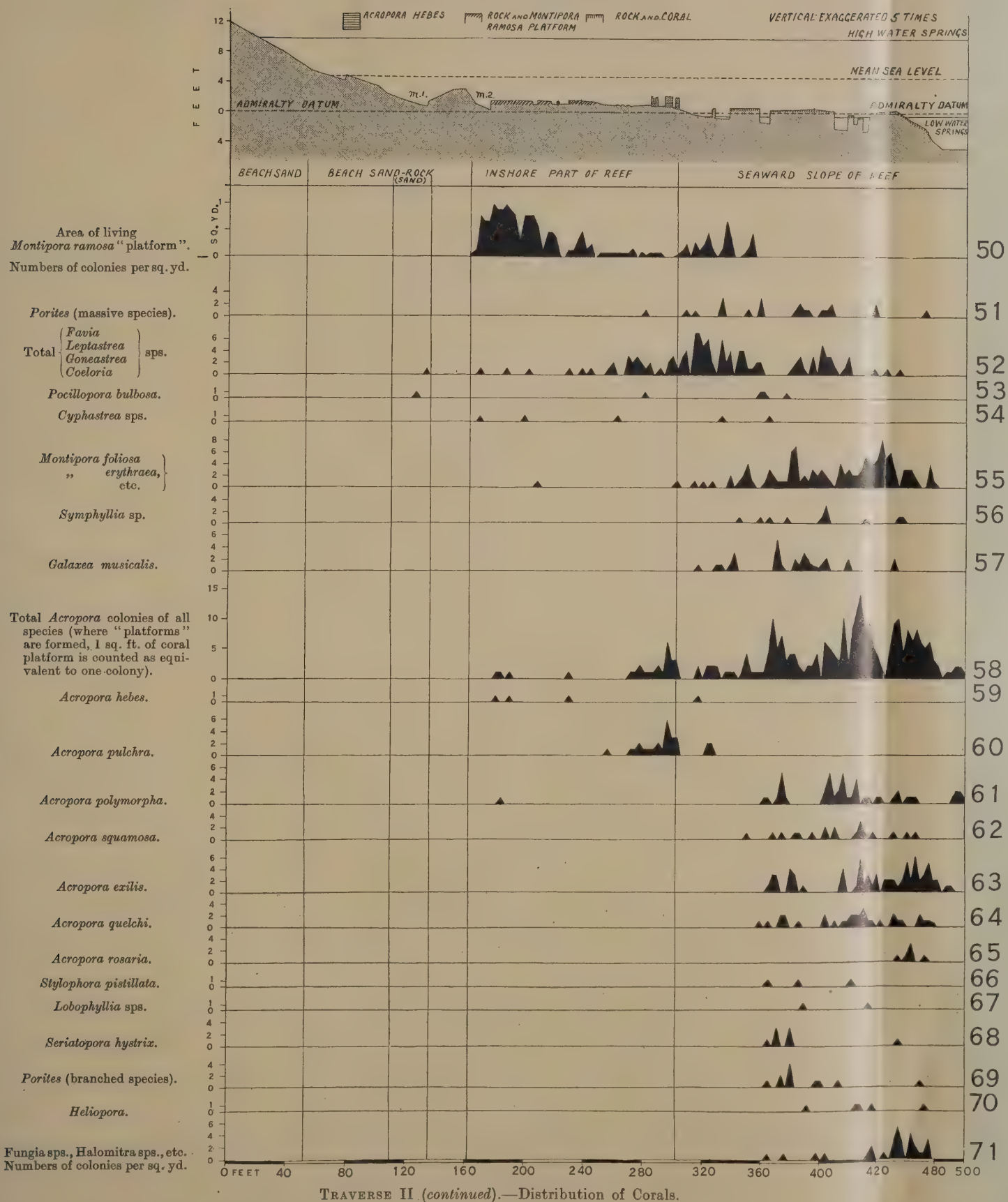
Brit. Mus. (Nat. Hist.).

REPORTS, VOL. III, No. 10.

PLATE VI.



NOTE.—Where possible the numbers of separate plants per square yard are given; where this is not possible, the distribution is recorded in terms of presence or absence per square yard, a wide black area signifying greater abundance than a narrow black area.



DESCRIPTION OF PLATE IX.

Large-scale map of an area in the deeper part of the WESTERN MOAT where coral growth for the moat is at a maximum. Scale 1/18. The area is crossed by Traverse I between 558 and 569 feet. (See Level Section and Text-fig. 1.)

Water to a depth of about 0·7 feet is held up at low water over the sand (black). The dead coral rock (grey and stippled) is darker and lighter in tone at lower and higher levels respectively; the higher parts of such rock lie at the surface level of low water, all other parts being well submerged. A key to the corals is given at the side. Algae were few, and too small to represent graphically.

Coral growth is here active, and at times has covered much of the bottom. Now much dead coral rock provides sites for the attachment and growth of fresh colonies. The upward growth of all corals is checked about low-water level, giving platforms with flat tops of the branching *M. ramosa* and of the massive growth forms of *Porites* and *Favia*. The tops of the massive corals are frequently dead, either entirely, or over a small central area on the smaller colonies. The large rounded block of coral rock about 4 feet in diameter on the left-hand side represents the dead remains of a flat-topped platform of a massive coral. It now serves as an attachment for fresh coral growth, both at the sides and also on the top, where it has been worn away to a sufficient depth below low-water level.

Key to species of *Favia*, etc., indicated by numbers on the map :

- | | |
|-----------------------------------|----------------------------------|
| 1. <i>Goniastrea retiformis</i> . | 6. <i>Goniastrea pectinata</i> . |
| 2. <i>Leptastrea roissiana</i> . | 7. <i>Favia astraiformis</i> . |
| 3. <i>Favia abdita</i> . | 8. „ <i>halicora</i> . |
| 4. „ <i>doreyensis</i> . | 9. <i>Coeloria daedalea</i> . |
| 5. „ <i>favus</i> . | |



1 2 3 4 5 feet.

KEY.



Montipora ramosa.



Flat-topped "platform" of
Montipora ramosa.



Dead *Montipora ramosa* "plat-
form".



Massive *Porites*.



Favia, etc. (central number indi-
cates species; see legend).



Psammocora gonagra.



Pocillopora bulbosa.



Acropora sps.



Montipora foliosa, etc.



Symphyllia.



Coeloria.



Platygyra.



Tridacna crocea.



Coral rock.



Water covering sand.

DESCRIPTION OF PLATE X.

Large-scale map of an area in the MADREPORE MOAT. Scale 1/18. The position of this area is seen in Text-fig. 1. It lies inside the ring marked in the Madreporo Moat.

This area may be compared with that shown in Plate I of the Western Moat. Here in the Madreporo Moat the depth of water (0.6 feet) held up at low water over the sand (black) is slightly less than that in the Western Moat (0.7 feet over the region seen in Plate I), and the physical conditions in the two regions are very similar. Corals here are less varied and abundant, and the plants are more numerous. Almost all the corals are living. Extensive platforms of *M. ramosa* and *Acropora hebes* are present, and massive growths of *Porites*, which have not yet reached low-water level, and are thus entirely living and not flat-topped. Unlike the Western Moat, there is very little dead coral material or coral rock (stippled grey) upon which other corals and algae may be attached. Algae are conspicuous and are attached to the few rocks present, and the expansive sandy areas (black) support an abundance of *Thalassia Hemprichii*. The larger animals lying on the sand and elsewhere are also shown: the blue starfish, *Linkia laevigata*, two clams, *Tridacna derasa* (left-hand side) and *T. crocea* boring in the coral rock, and *Synapta maculata*.

It is possible that this area now shows a young stage of a moat fauna and flora, and that the Western Moat mapped in Plate I shows an older stage of the same formation. Further growth of the corals now seen in Plate II would lead to the formation of flat-topped platforms of massive corals of increasing size, and the sandy bottom would become more and more covered by coral growth, resulting in the exclusion of many of the plants. Death of the larger massive forms would lead to the state seen in Plate I.

Key to species of *Favia*, etc., indicated by numbers on the map:

3. *Favia abdita*.

6. *Goniastrea pectinata*.

7. *Favia astraeiformis*.



1 2 3 4 5 6 feet.

KEY.



Montipora ramosa.



Flat-topped "platform" of
M. ramosa.



Massive *Porites*.



Favia, etc. (central number indi-
cates species; see legend).



Pocillopora bulbosa.



Acropora hebes.



Tridacna crocea burrowing in
rock.



Coral rock.



Thalassia Hemprichii growing in
sand.



Padina.



Turbinaria.



Sargassum lanceolatum.

DESCRIPTION OF PLATE XI.

(a) Large-scale map of an area on the SEAWARD SLOPE crossed by Traverse I between 892 and 961 feet (see level section). Scale 1/18.

Coral growth on Traverse I is here at a maximum, and the region is dominated by species of *Acropora*. The level of water changes directly with the state of the tide. The sandy bottom (black) lies at about 2 feet below datum level. The coral rock (stippled grey) is darker in tone at lower levels. The top of the boulder shown in the upper part of the plate rises almost to datum level. Its upper surface bears massive colonies of *Favia*, etc., and the burrowing clam *Tridacna crocea*; while on the steeper sides brackets of Acropores and other branching corals project one above another. Only parts of such brackets can be seen in a view from above. The top of the rock on the lower part of the plate is at a deeper level, only just above that of the sand, and bears a great variety of corals and some alcyonaria on its surface.

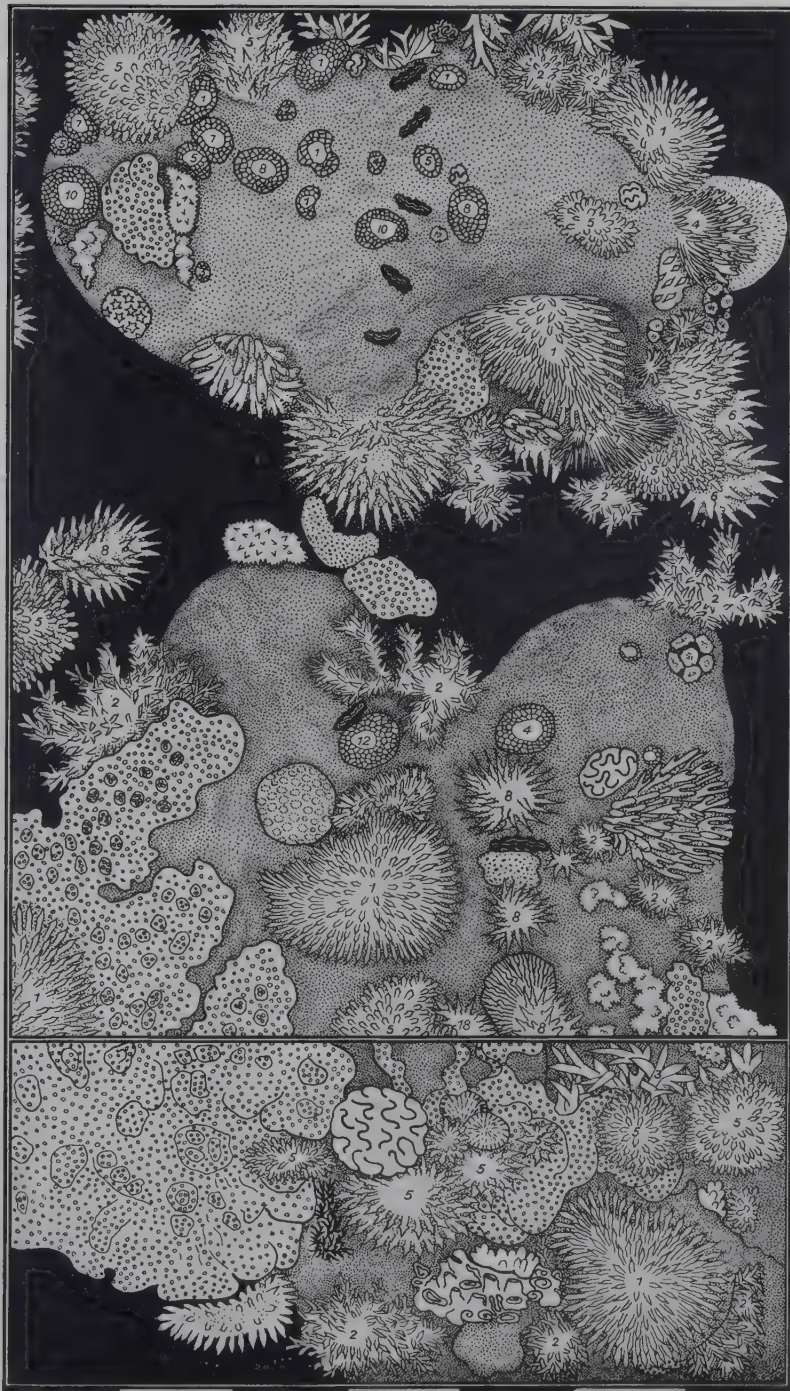
(b) Large-scale map of an area on the SEAWARD SLOPE crossed by Traverse II between 366 and 373 feet, and situated just beyond pool 2 (see level section). Scale 1/18.

Coral growth here is particularly abundant. Dead coral rock (stippled grey) rises to just above datum level from a sandy pool (black) with a bottom level of 1·4 feet below datum. The rock is almost completely covered by a large variety of corals, eleven species being present over 2 square yards.

Key to species indicated by numbers on the map :

<i>Favia</i> , etc.	<i>Acropora</i> .
1. <i>Goniastrea retiformis</i> .	1. <i>Acropora squamosa</i> .
5. <i>Favia favius</i> .	2. „ <i>exilis</i> .
7. „ <i>astraciformis</i> .	3. „ <i>polymorpha</i> .
8. „ <i>halicora</i> .	4. „ <i>hebes</i> .
10. <i>Goniastrea</i> K. 5.*	5. „ <i>quelchi</i> .
	6. „ <i>gemmifera</i> .
	7. „ <i>hyacinthus</i> .
	8. „ <i>variabilis</i> .

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.



1 2 3 4 5 6 feet.

KEY.

- Porites* branched in (b); massive in (a and b).
- Favia*, etc. (central number indicates species; see legend).
- Pocillopora danae*.
- Acropora* (central number indicates species; see legend).
- Montipora foliosa*,
" *erythraea*, etc.
- Symphyllia*.
- Lobophyllia*.
- Platygyra*.
- Galaxea fascicularis*.
- Stylophora pistillata*.
- Orbicella*.
- Astreopora*.
- Goniopora*.
- Merulina*.
- Pavona*.
- Echinopora*.
- Millepora*.
- Alcyonium pachyclados*.
- Seriatopora* and *Tridacna crocea*
in rock. Sand (black).

DESCRIPTION OF PLATE XII.

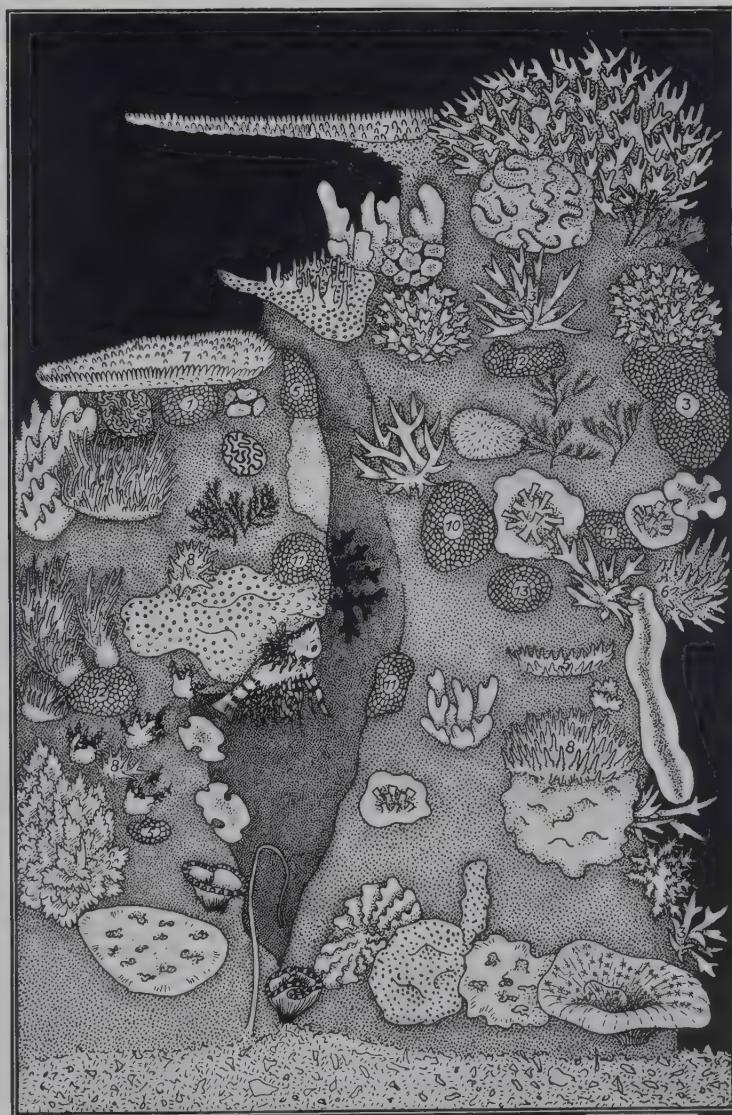
Large-scale map of part of the vertical face of a CORAL HEAD situated off the north-east corner of Low Isles in line with beacons C and B (Text-fig. 2), and marked at "X" in Text-fig. 2*b*. Scale 1/18.

The top of the coral head rises almost to datum level, and the sea floor, composed of sand and shingle, lies at 9-10 feet below datum. Water is represented by black and the rock by stippled grey areas. No mud lies on the rocks or on the shingle of the sea floor. The side of the coral head is well covered by corals comprising a large variety of genera and species (compare the rich coral zone seen in Plate III, where the rock is more overgrown by corals, but not so many different forms are present). Coral growth persists to the base of the coral head, where encrusting or flattened colonies of *Echinopora* and *Porites* and funnel-shaped *Turbinaria* and *Podobacia* are present. *Millepora* of various growth forms is more frequent here than in the other types of coral area which are shown in Plates IX-XI, and becomes more finely branched towards the top of the coral head. At the top of the rock horizontal projecting brackets of *Acropora hyacinthus* and *Montipora erythraea* occur much as on the coral heads situated just inside the outer barrier reefs. A black *Dendrophyllia* is seen growing in a poorly-illuminated situation on the rock, as is usual on Low Isles. Alcyonaria on this rock are also frequent and varied; *Spongodes* and *Juncea* growing near the base are not found in the shallower regions about Low Isles. The Hydroid, *Aglaophenia*, is large and frequent. In shallower situations hydroids are usually very small and fewer.

Key to species indicated by numbers on the map:

- | <i>Favia</i> , etc. | <i>Acropora</i> . |
|--------------------------------------|---------------------------------|
| 1. <i>Goniastrea retiformis</i> . | 3. <i>Acropora polymorpha</i> . |
| 3. <i>Favia abdita</i> . | 6. " <i>gemmifera</i> . |
| 5. " <i>favus</i> . | 7. " <i>hyacinthus</i> . |
| 10. <i>Goniastrea</i> K. 5.* | 8. " <i>variabilis</i> . |
| 11. <i>Leptastrea ehrenbergana</i> . | |
| 12. <i>Favia clouei</i> . | |
| 13. " <i>laxa</i> . | |

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.



KEY.

*Massive Porites.**Favia*, etc. (central number indicates species; see legend).*Psammocora gonagra.**Pocillopora danae.**Acropora* (central number indicates species; see legend).*Montipora* spp.*Symphyllia.**Lobophyllia.**Platygyra.**Echinopora.**Turbinaria.**Dendrophyllia.**Podobacea.**Astreopora.**Millepora* (coarse branches).*Millepora* (fine branches).*Millepora* (encrusting)*Sinularia polydactyla.*1 *Dendronephthya spinifera.*2 *Nephthya mollis.*3 *Juncea.*4 *Aglaophenia.*5 *Sarcophyton trocheliophorum.*6 *Lobophytum crassum.*7 *Sinularia flexibilis.*

8 Coral rock standing on sea-floor of coral debris, water black.

DESCRIPTION OF PLATE XIII.

Large-scale map of two areas close together situated near Traverse II on the landward part of the SEAWARD SLOPE (see level section and Text-fig. 2), where alcyonaria are particularly abundant. Scale 1/18.

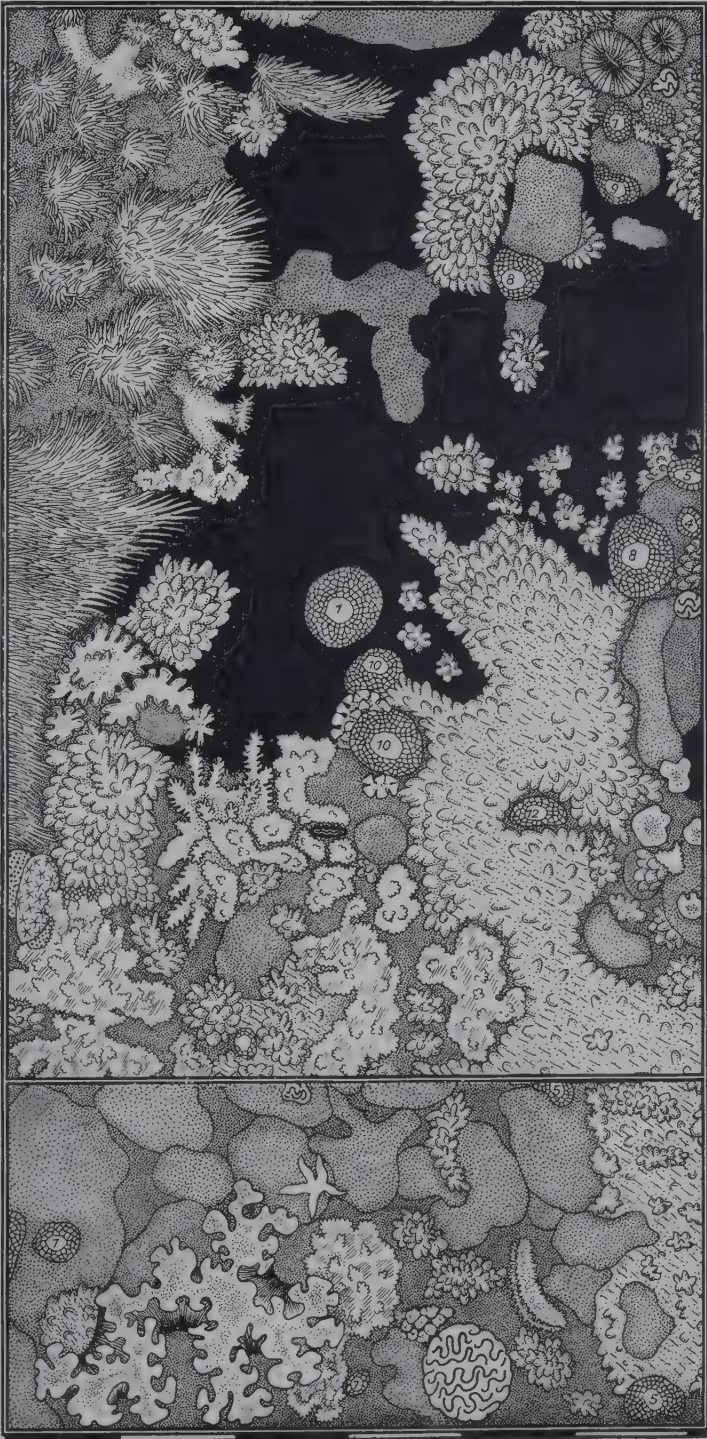
The level of the sand (black) is about 1 foot below datum. Coral rock very much worn (stippled grey) lies well below datum level, and the living and semi-dead colonies of *M. ramosa* rise a little above datum level. The Fungidae, which become abundant on the Seaward Slope, are here present, and the alcyonaria are abundant and varied.

Sinularia flexibilis is seen in various stages of expansion. The underlying rock is only exposed when the colonies are contracted, as in the upper left-hand corner of (a). A large specimen of *Sarcophyton trocheliophorum* in the contracted state is seen in (b). The larger animals present are also shown: the boring clam *Tridacna crocea*, the blue starfish *Linkia* and the holothurian *Stichopus*.

Key to species indicated by numbers on the map:

- | | |
|-----------------------------------|-------------------------------|
| 1. <i>Goniastrea retiformis</i> . | 8. <i>Favia halicora</i> . |
| 4. <i>Favia doreyensis</i> . | 9. <i>Coeloria daedalea</i> . |
| 5. „ <i>favus</i> . | 10. <i>Goniastrea</i> K. 5.* |
| 7. „ <i>astraeiformis</i> . | 12. <i>Favia clouei</i> . |

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.



KEY.

-  *Montipora ramosa*.
-  Dead *Montipora ramosa*.
-  *Porites* (massive).
-  *Pocillopora*.
-  *Symphyllia*.
-  *Lobophyllia*.
-  *Fungia*.
-  *Halomitra*.
-  *Galaxea*.
-  *Sinularia flexibilis*.
-  *Sarcophytum trocheliophorum*.
-  *Lobophytum crassum*.
-  *Sinularia* sp.
-  *Sinularia polydactyla*.
-  *Alcyonium pachyclados*.
-  *Lobophytum* sp.
-  Rock and sand (black).

1 2 3 4 5 6 feet.

Adlard & Son, Ltd, Impr.

DESCRIPTION OF PLATE XIV.

Large-scale map of an area on the REEF CREST of Yonge Reef, one of the Outer Barrier Reefs. (For position of the various regions of Yonge Reef see Vol. III, No. 2, Text-fig. 5, and Plate XVII, fig. 2.) Scale 1/18.

The area is dry at low tide, and shows a limited amount of coral growth on a smooth and level substratum of coral rock covered with a veneer of pink nullipores (black ruled with white). Two starfish, *Linkia gouldingii*, lie on the rock. For further description of the area see p. 304.

Key to species indicated by numbers on the map :

<i>Favia</i> , etc.	<i>Acropora</i> .
1. <i>Goniastrea retiformis</i> .	4. <i>Acropora hebes</i> .
3. <i>Favia abdita</i> .	5. " <i>quelchi</i> .
9. <i>Coeloria</i> sp.	6. " <i>gemmifera</i> .
10. <i>Goniastrea</i> K. 5.*	7. " <i>hyacinthus</i> .
11. <i>Leptastrea ehrenbergana</i> .	9. " <i>pulchra</i> .
12. <i>Favia clouei</i> .	10. " <i>rosaria</i> .
13. " <i>laza</i> .	11. " <i>decipiens</i> .
14. " <i>wakayana</i> .	

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.



Key.



Favia, etc. (central number indicates species; see legend).



Massive *Porites*.



Encrusting *Montipora*.



Grey *Zoanthid*.



Smooth rock covered by nullipores.



Rock at a lower level



Tubipora.



Dead coral.



Millepora.



Pocillopora verrucosa.



Acropora (number and conventions indicate species; see legend).



Acropora decipiens.



Hydnothophora.



Sponge, *Phyllospongia ridleyi*.



Green alga, *Chlorodesmis comosa*.

1 2 3 4 5 6 7 8 feet.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XV.

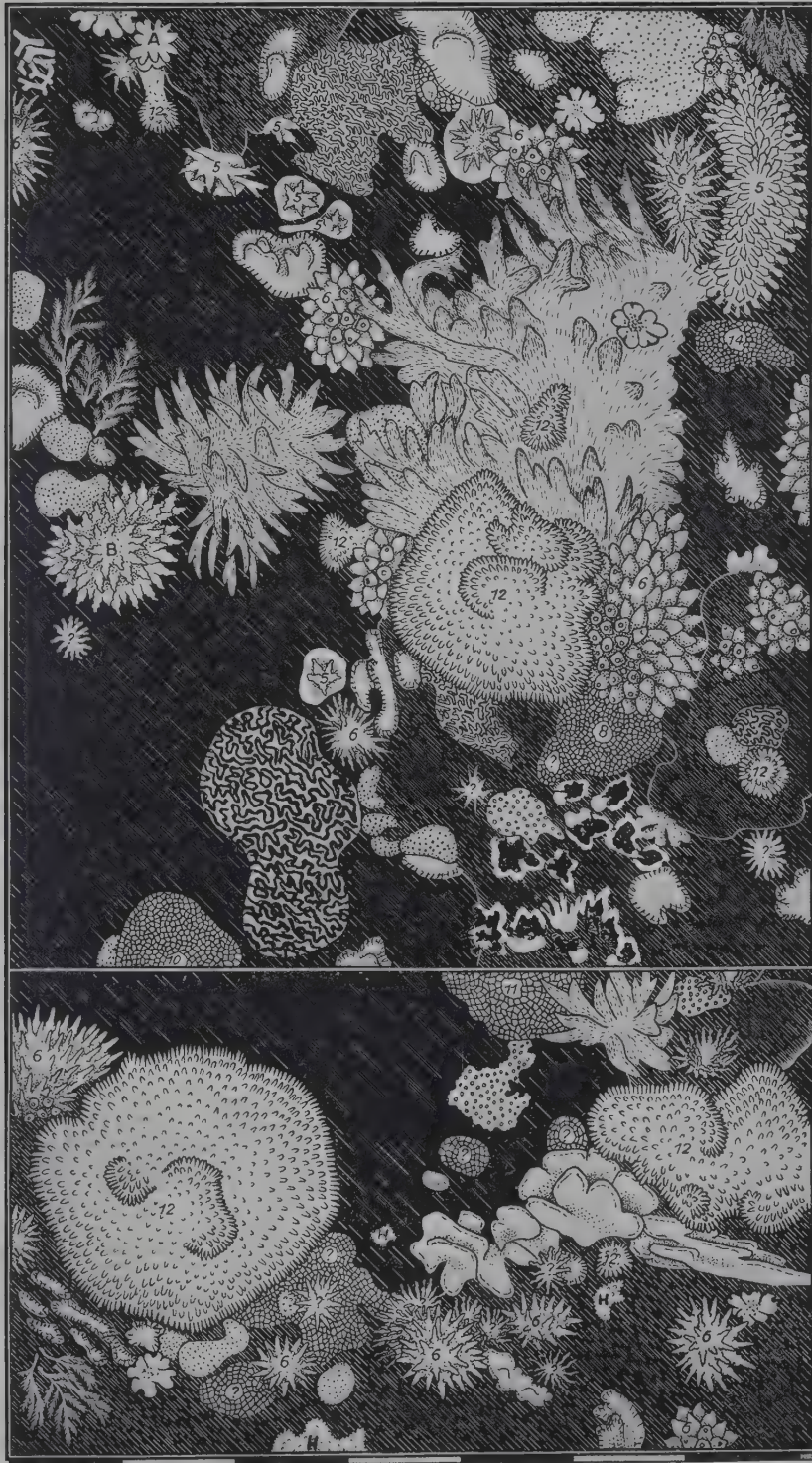
Large-scale maps of two areas in the OUTER MOAT of Yonge Reef, one of the Outer Barrier Reefs. (For position of the various regions of Yonge Reef see Vol. III, No. 2, Text-fig. 5, and Plate XVII, fig. 2.) Scale 1/18.

The rocky substratum, hard and smooth and covered with a veneer of nullipores, is not so level as on the Reef Crest. The left half of the upper area, and the top half of the lower area, lie at a lower level than the rest of these areas, and are covered with about 1 foot of water. The remaining rock is higher, and projects out of the water in places. Corals are luxuriant and soft Alcyonaria few. For further description of these areas see p. 305.

Key to species indicated by numbers on the map :

<i>Favia</i> , etc.	<i>Acropora</i> .
8. <i>Favia halicora</i> .	5. <i>Acropora quelchi</i> .
10. <i>Goniastrea</i> K. 5.*	6. „ <i>gemmifera</i> .
11. <i>Leptastrea ehrenbergana</i> .	12. „ <i>hyacinthus</i> .
14. <i>Favia wakayana</i> .	13. „ <i>delicatula</i> .
	„ <i>decipiens</i> (separate convention).

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.



KEY.

-  *Favia*, etc. (central number indicates species; see legend).
-  Massive *Porites*.
-  Encrusting *Montipora*.
-  *Acropora palifera*.
-  *Pocillopora verrucosa*.
-  *Pocillopora eydouzi*.
-  Encrusting *Millepora*.
-  *Hydnophora*.
-  *Platygyra*.
-  *Coeloria*.
-  *Acropora hyacinthus*, etc.
-  *Acropora decipiens*.
-  *Acroporus* (central number indicates species; see legend).
-  Branching *Millepora*.
-  Higher levels } Rock covered by nullipores.
Lower levels }
-  *Phyllospongia ridleyi*.
-  *Aglaophenia cupressina*.
-  *Nephthya mollis*.
-  *Paralemnalia thyrsoidea*.

1 2 3 4 5 6 7 feet.

Adlard & Son, Ltd., Impr.

DESCRIPTION OF PLATE XVI.

Large-scale maps of areas on the INNER PARTS of Yonge Reef, one of the Outer Barrier Reefs. (For position of the various regions of Yonge Reef see Vol. III, No. 2, Text-fig. 5, and Plate XVII, fig. 2.) Scale 1/18.

The upper area lies in the ANCHORAGE CORAL ZONE. Pools of water (black) about 4 feet deep over sand lie among irregular masses of coral rock (stippled grey). The rock is not so strongly incrustated with nullipores as in the preceding areas, and it bears a rich and varied coral fauna. Fish abound in the pools. For further description see p. 306.

The lower area lies at the edge of a CORAL HEAD in the Zone of Coral Heads lying leeward of the Anchorage Coral Zone. This area differs from the last in that the water lies at a depth of 4-5 fathoms, so that large stag-horn-like growths of acropores can find place in the open water, and the tops of the coral rock masses are richly covered by corals, particularly conspicuous being the dish-shaped *Acropora hyacinthus*, etc., and the coarse form of *Acropora gemmifera*. Compare also with the Low Isles coral head on Plate XII.

Key to species indicated by numbers on the map :

<i>Favia</i> , etc.	<i>Acropora</i> .
1. <i>Goniastrea retiformis</i> .	5. <i>Acropora quelchi</i> .
3. <i>Favia abdita</i> .	6. „ <i>gemmifera</i> , stout and fine varieties.
5. „ <i>favus</i> .	12. „ <i>hyacinthus</i> , etc.
8. „ <i>halicora</i> .	„ <i>palifera</i> (separate convention).
10. <i>Goniastrea</i> K. 5.*	„ spp. large stag-horn growths (separate convention).
15. <i>Favia vasta</i> .	
X. Unidentified, but occurs on Low Isles coral heads also.	

* This species could not be satisfactorily determined, and is so labelled in the collection deposited in the British Museum.

KEY.

-  *Favia*, etc. (central number indicates species: see legend).
-  Massive *Porites*.
-  *Goniopora*.
-  *Galaxea*.
-  *Stylophora*.
-  *Pocillopora verrucosa*.
-  *Pocillopora danae*,
" *bulbosa*.
-  *Millepora*.
-  *Seriatopora*.
-  *Fungia*.
-  *Acropora quelchi*.
-  *Acropora palifera*.
-  *Acropora hyacinthus*.
-  *Acropora gemmifera*, stout and
slender growth forms.
-  Large "stag-horn" *Acroporas*.
-  Rock.
-  Sand covered by several feet of
water.
-  Dead corals.
-  Green alga, *Chlorodesmis comosa*.

